Age Determination and Growth in the Male South African Fur Seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae) Based upon Skull Material

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Skull remains are the most commonly found material of marine mammals and the most likely to be kept in natural history collections. Morphology, relative size and growth of the skull in 83 South African fur seals, *Arctocephalus pusillus pusillus*, from the coast of southern Africa are described. The South African or Cape fur seal is very closely related to the Australian fur seal (*Arctocephalus pusillus doriferus*). Age structure of populations is important in understanding the conservation status of an animal population and the impacts of human activity upon the survival of viable wild populations of animal species. Skull measurements (n = 32 variables) were examined in relation to standard body length (SBL - defined as the length from the nose to the tail in a straight line with the animal on its back), condylobasal length (CBL) and chronological age (y) using linear regression. Animals ranged from 10 months to ≥ 12 y (12^+ y). Twenty four animals were of known-age, while 39 were aged from counts of incremental lines observed in the dentine of tooth sections. Morphological observations were generally consistent with earlier studies. Condylobasal length was highly, positively correlated with SBL and age. Overall, skull variables grew at a slower rate than SBL, apart from height of mandible at meatus and angularis to coronoideus, which expressed isometry relative to SBL. Condylobasal length continued to increase until at least 12 y, with no obvious growth spurt between 8–10 y, when social maturity (full reproductive capacity) is attained. Mean CBL was 19.4% of SBL in yearlings; 15.5% in subadults, and 13.7% in adults. Apart from the dentition, all variables of the facial skeleton followed a somatic growth trajectory. Most variables expressed positive allometry relative to CBL, with greatest growth occurring in the vertical part of the mandible. Mastoid breadth, and gnathion to middle of occipital crest, expressed a strong secondary growth spurt at 10 y. Breadth of brain case, and basion to bend of pterygoid, followed a neural growth trajectory, scaling with negative slope relative to CBL. Sutures of the brain case (i.e., basioccipito-basisphenoid, occipito-parietal, interparietal and coronal) closed before those of the facial skeleton. Condylobasal length was found to be a 'rough indicator' of SBL and age group (adult, subadult), but not of absolute age. Suture age was not a good indicator of absolute age or age group. A comparison is finally made between skull data on the South African fur seal (*A. pusillus pusillus*) with available data on the Australian fur seal (*A. pusillus doriferus*).

AGE AND GROWTH IN SOUTH AFRICAN FUR SEAL SKULLS

INTRODUCTION

Skull remains are the most commonly found material of marine mammals and the most likely to be kept in natural history collections. It would be useful to be able to gain as much information as possible about sex, age, probable size, breeding status and even in many cases positive identification of such material in terms of modern taxonomy and nomenclature (Brunner 2003). The South African or Cape fur seal (*Arctocephalus pusillus pusillus*) occurs on the Namibian and South African coasts and nearby offshore islands (Schaffer, 1958; King, 1983; Warneke and Shaughnessy, 1985) but does not occur on Subantarctic Islands between Africa and Australia. The South African fur seal and the Australian fur seal (*Arctocephalus pusillus doriferus*) are now regarded as closely related varieties of the same species (*Arctocephalus pusillus*) (King 1972; King 1983; Wynen et al., 2001; Brunner et al., 2002; Brunner 2003). Historically, the Australian fur seal was found on the southern Australian coast from Kangaroo Island (South Australia) to Seal Rocks (mid coast NSW) with its distribution centred on Bass Strait and Tasmania (King 1969). The identity of the fur seals that originally inhabited Macquarie Island until wiped out in the early 19th century is uncertain. Today breeding colonies are more or less restricted to islands of the Bass Strait region and Tasmania (Kirkwood et al., 1992; Arnould, and Warneke, 2002; Shaughnessy et al., 2002; Arnould et al., 2003).

It is useful to as fully as possible investigate morphometric measurements of seal skulls to correlate with age and maturity and breeding status. Earlier cranial growth studies in pinnipeds were based on unreliable age determination techniques, including: (i) the extent of closure of cranial sutures; (ii) body length, colour of vibrissae, pelage and general appearance; (iii) ovarian structure; and (iv) baculum development (e.g. Doutt, 1942; Rand, 1949a, b, 1950, 1956; King 1969; King 1983; Brunner 1998ab; Brunner et al., 2002; Brunner et al., 2004; Daneri et al., 2005). A common feature of most of these studies is the limited number of specimens available and the unknown age of most of the material. Therefore, observed growth patterns could not be quantified with any real meaning (King, 1972); generally a division into mature and immature animals was all that was possible (King 1969; King 1983). Fortunately a reasonably precise method of age determination of untagged South African fur seals has been established from incremental growth lines in the pulp of teeth (Scheffer, 1950; Laws, 1953; McCann, 1993; Oosthuizen, 1997) but this involves destructive sampling of material which might not be negotiable on museum material. Dentition was also used for aging 69 male and 163 female Australian fur seals collected from an island in Bass Strait in 1970-1972, but unfortunately the skulls were not measured as part of the study (Arnould and Warneke 2002).

Within the Otariidae, information on cranial and mandibular growth based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), is only available for a small number of species including *Callorhinus ursinus*, northern fur seal (Scheffer and Wilke, 1953); *Zalophus californianus*, California sea lion (Orr et al., 1970); and *Eumetopias jubatus*, northern (Steller) sea lion (Fiscus, 1961; Winship, Trites and Calkins 2001). Sometimes very few skull variables have been recorded. Currently, there is limited information on cranial growth according to age (y) in southern hemisphere fur seals: the main problem being small sample sizes (King 1969; King 1983; Brunner 1998ab; Brunner et al., 2002; Brunner et al., 2004; Daneri et al., 2005), particularly the small numbers of tagged individuals of known age that are available.

In the mammalian skull, there are two growth models, neural and somatic, each with two types of growth, monophasic and biphasic (Todd and Schweiter, 1933; Scott, 1951; Moore, 1981; Sirianni and Swindler, 1985). In neural growth, skull components associated with the nervous system (i.e., braincase, orbital and otic capsules) grow rapidly during prenatal and early postnatal life, completing most of their growth well before the rest of the body (Moore, 1981). In somatic growth, all other skull components (i.e., facial skeleton) follow a more protracted growth course (Moore, 1981). After the initial growth spurt experienced during early development, growth may be reasonably constant (monophasic growth), or there may be a secondary growth spurt in older animals (biphasic growth) when they reach sexual maturity. Brunner (1998a) and Brunner et al. (2004) drew the overall conclusion that growth patterns in fur seal skulls were similar to that found in other carnivores such as canids (dogs) (Wayne, 1986; Morey, 1990; Evans, 1993) and other marine mammals (Bryden, 1972).

Current populations of South African fur seals number more than 2 million individuals although they reached a low level of about 100,000 early in the 20 th century. Their larger populations, occasional culling, drowning in fishing nets and shooting of "problem" animals, have made more specimens available for study than their Australian relatives (*A. pusillus doriferus*). Furthermore, another consequence of the much smaller populations of Australian fur seals (about 35,000 – 60,000: Kirkwood et al., 1992; 67,000 – 200,000, Shaughnessy et al., 2002; Arnould and Warneke 2002; Arnould et al., 2003) and more limited accessibility is that very little cranial morphometric data are available on Australian fur seals (King 1969; Brunner 1998ab), particularly of definitively known ages based on tagged individuals (Brunner 1998ab,

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Arnould and Warneke 2002).

Here we examine the skulls of 83 male South African fur seals, *Arctocephalus pusillus pusillus*, from southern Africa. Specific objectives were to: (i) describe the general morphology of the skull; (ii) quantify growth of skull measurements ($n = 32$ variables) relative to standard body length ($n = 74$ animals), condylobasal length ($n = 83$ animals) and chronological age ($n = 63$ animals); and (ii) determine if condylobasal length and suture closure are useful indicators of age and/or standard body length. This is a very large data set compared to recent studies on the Antarctic fur seal (*Arctocephalus gazella*) and Southern fur seal (*A. australis*) (Daneri et al., 2005), the Australian fur seal (*A. pusillus doriferus*) (King 1969; Brunner 1998ab) and the New Zealand fur seal (*A. australis forsteri*: King 1969; Brunner 1998ab) and the recent review of cranial ontogeny of otariid seals by Brunner et al. (2004).

A limited comparison is also made between the available data on the South African fur seal from the present study with published material from King (1969) and from Brunner (1998ab, 2000) on Australian fur seals. Modern multivariate morphometric analyses of skull parameters complete data sets rather than just means and variances of variables need to be available.

MATERIALS AND METHODS

Collection of specimens

South African fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34° 03'S, 23° 24'E) and East London (33° 03'S, 27° 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). The circumstances under which most specimens were obtained are listed in Appendix 1. Apart from specimens collected before May 1992 ($n = 16$), all specimens were collected by the first author. One animal (PEM2238) was collected NE of the study area, at Durban. From this collection, skulls from 59 males were selected for examination (Appendix 1).

The sample was supplemented with measurements from 24 skulls collected by staff from Marine and Coastal Management (MCM), Cape Town, South Africa. These skulls were from males that had been tagged as pups, and were therefore of known-age (1–12 y). They were collected from the west coast, south west coast, south coast and the Eastern Cape Province of South Africa, between February 1984 and July

1997. The date of collection, method of collection and approximate location of specimens are listed in Appendix 1. MCM seal specimens are accessioned as AP followed by a number in Appendix 1.

East Coast and West Coast Animals

Additional skulls from Sinclair Island (West coast of southern Africa, 27° 40'S, 15° 31'E) were measured (condylobasal length only) to determine if Eastern Cape seals ($n = 28$ males) were of similar size to those inhabiting west coast waters ($n = 12$ males). PEM animals were adults 7– ≥ 12 y. West coast animals were adults of undocumented-age. West coast animals were collected by Dr R. W. Rand in the 1940s and housed in the South African Museum, Cape Town. These skulls were divided into sub-adult or adult classes based upon size and suture criteria (see below).

Preparation and measurement of skulls

Skulls were defleshed and macerated in water for 2–3 months. Water was changed regularly. Skulls were then gently washed in mild detergent (or brushed with water), and air dried at room temperature. A small number of skulls were defleshed and gently boiled. Dry specimens were measured ($n = 32$ linear measurements) to the nearest 0.5 mm using a vernier calliper (Table 1, Figure 1).

Variables used largely correspond to those reported in earlier otariid studies (Sivertsen, 1954; Orr et al., 1970; Repenning et al., 1971; Kerley and Robinson, 1987; Daneri et al., 2005; Brunner et al., 2004; Brunner et al., 2004) and in particular the studies of Brunner (1998ab) focusing on the Australian fur seal (*A. pusillus doriferus*). Care was taken to measure standard parameters, measured in the same way as described in previous studies. Variables were grouped by region in an attempt to reflect a functional cranial analysis and to assess overall skull size (Hartwig, 1993) (Table 1). All PEM measurements (and measurements taken form Sinclair Island skulls) were recorded by the first author. The majority of MCM measurements were recorded by the third author (M.A. Meÿer).

Suture index

Eleven cranial sutures (Figure 2) from 48 skulls were examined and assigned a value 1-4, according to the degree of closure (1 = suture fully open; 2 = open; 3 = suture half closed; 4 = suture closed), according suture index (SI), ranging from 11 (all fully open) to 44 (all sutures closed). These values were added to give a total suture index (SI), ranging from 11 (all fully open) to 44 (all sutures closed). The suture

Table 1: Linear skull measurements (n = 32) taken from male South African fur seals in this study. Measurements illustrated in Figure 1. Note that L26 and L27 were difficult to measure accurately. Parameters are broadly associated with the following functions; A- articulation, BC – braincase, F – feeding, R/V – respiration/vocalisation.

Code	Variable	Region of Skull	Function
Dorsal			
D1	Condylobasal length (posterior point on the occipital condyles to the most anterior point on the premaxilla)	–	–
D2	Gnathion to middle of occipital crest	–	R/V
D3	Gnathion to posterior end of nasals	splanchnocranium	R/V
D4	Greatest width of anterior nares (distance between the anterior margins of the nares)	nasal	R/V
D5	Greatest length of nasals (distance between the anterior and posterior margins of nasals)	nasal	R/V
D6	Breadth at preorbital processes	–	–
D7	Least interorbital constriction	frontal	–
D8	Greatest breadth at supraorbital processes	frontal	F
D9	Breadth of brain case (at the coronal suture, anterior to the zygomatic arches)	neurocranium	BC
Palatal			
P10	Palatal notch to incisors (posterior margin of first incisor alveolus to palatal notch, excluding cleft)	palate	R/V, F
P11	Length of upper postcanine row (anterior margin of postcanine one alveolus to the most posterior margin of postcanine six alveolus)	palate (dentition)	F
P12	Greatest bicanine breadth	palate	R/V, F
P13	Gnathion to posterior end of maxilla (palatal)	palate	R/V, F
P14	Breadth of zygomatic root of maxilla	zygomatic arch	F
P15	Breadth of palate at postcanine 1 (excluding the alveoli)	palate	F
P16	Breadth of palate at postcanine 3 (excluding the alveoli)	palate	F
P17	Breadth of palate at postcanine 5 (excluding the alveoli)	palate	F
P18	Gnathion to posterior border of postglenoid process	–	R/V, F
P19	Bizygomatic breadth (maximum distance between the lateral surfaces of the zygomatic arches)	zygomatic arch	F
P20	Basion to zygomatic root (anterior)	–	–
P21	Calvarial breadth (greatest transverse width across of the skull base, anterior to the mastoid)	basicranium	A
P22	Mastoid breadth (width across the processes)	basicranium	A, F
P23	Basion to bend of pterygoid (anterior of basion to anterior of pterygoid)	basicranium	BC, A, F

Table 1 (continued)

Code	Variable	Region of skull	Function
Lateral			
L24	Gnathion to anterior of foramen infraorbital (= lateral face length)	splanchnocranium	R/V
L25	Gnathion to posterior border of preorbital process	splanchnocranium	R/V
L26	Height of skull at base of mastoid (excluding crest)	–	
L27	Height of sagittal crest	neurocranium	BC, F
Mandibular			
M28	Length of mandible (posterior margin of condyle to anterior margin of the first incisor alveolus)	mandible	F
M29	Length of mandibular tooth row (anterior margin of the first incisor alveolus to the most posterior margin of postcanine five alveolus)	mandible (dentition)	F
M30	Length of lower postcanine row (anterior margin of post- canine one alveolus to the most posterior margin of post- canine five alveolus)	mandible (dentition)	F
M31	Height of mandible at meatus (dorsal margin of coronoid process to the base of the angularis)	mandible	A, F
M32	Angularis to coronoideus (dorsal margin of coronoid process to the top of the angularis)	mandible	F

numbering system and the method of judging degree of closure and calculation of the suture index follows Moore (1981). The suture index has been frequently and successfully used as a criterion for separating immature and mature skulls of mammals (Moore 1981), including seals (eg. Rand 1949; King 1969; Orr et al., 1970; Bryden, 1972; King 1972; Brunner 1998ab; Brunner et al., 2004; Daneri et al., 2005).

Age determination

The age of animals was estimated from counts of growth layer groups (GLGs) observed in the dentine of thin tooth sections (Scheffer, 1950). Upper canines were sectioned longitudinally using a circular diamond saw. Sections were ground down to 280–320 μm, dehydrated, embedded in resin and viewed using a stereomicroscope in polarised light (Oosthuizen, 1997). Each section was read by one individual five times, without knowledge of which animal was being examined (repeated blind counts). Ages were rounded off to the nearest birth date. The median date of birth was assumed to be 1 December (Arnould and Warneke 2002; Shaughnessy et al., 2002). The median of the five readings was used too estimate age. Outliers were discarded as reading errors.

The total number of aged animals (tagged known-age animals and canine aged animals) was 63. All MCM skulls (n = 24) were of known-age based on tagging. Of the 59 PEM animals in the study: (i) 28 were aged from counts of incremental lines observed in the dentine of upper canines as described in Schaffer (1950), i.e., range 1–10 y; (ii) 11 were identified as adults > 12 y (i.e., pulp cavity of the upper canine closed); and (iii) 20 could not be aged because of missing or decayed teeth. In South African fur seals, animals > 13 y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes at that age which terminates tooth growth, hence the age group '≥12 y or 12^+ y)'. Dentition has also been used to age Australian fur seals (Arnould and Warneke 2002) who claim that it is possible to age some male Australian fur seals to 17 years old based on upper canine dentition.

For this study, the following age groups were used: yearling (10 mo to 1 y 6 mo); subadult (1 y 7 months to 7 y 6 months); and adult (≥ 7 y 7 months) (Table 2). Unfortunately, no South African fur seals skulls were available from wild-tagged individuals with definitive ages greater than 12 y. The estimated longevity of South African fur seal males based upon zoo animals is $c.$ 20 y so it appears that they have a similar potential lifespan to the Australian variety
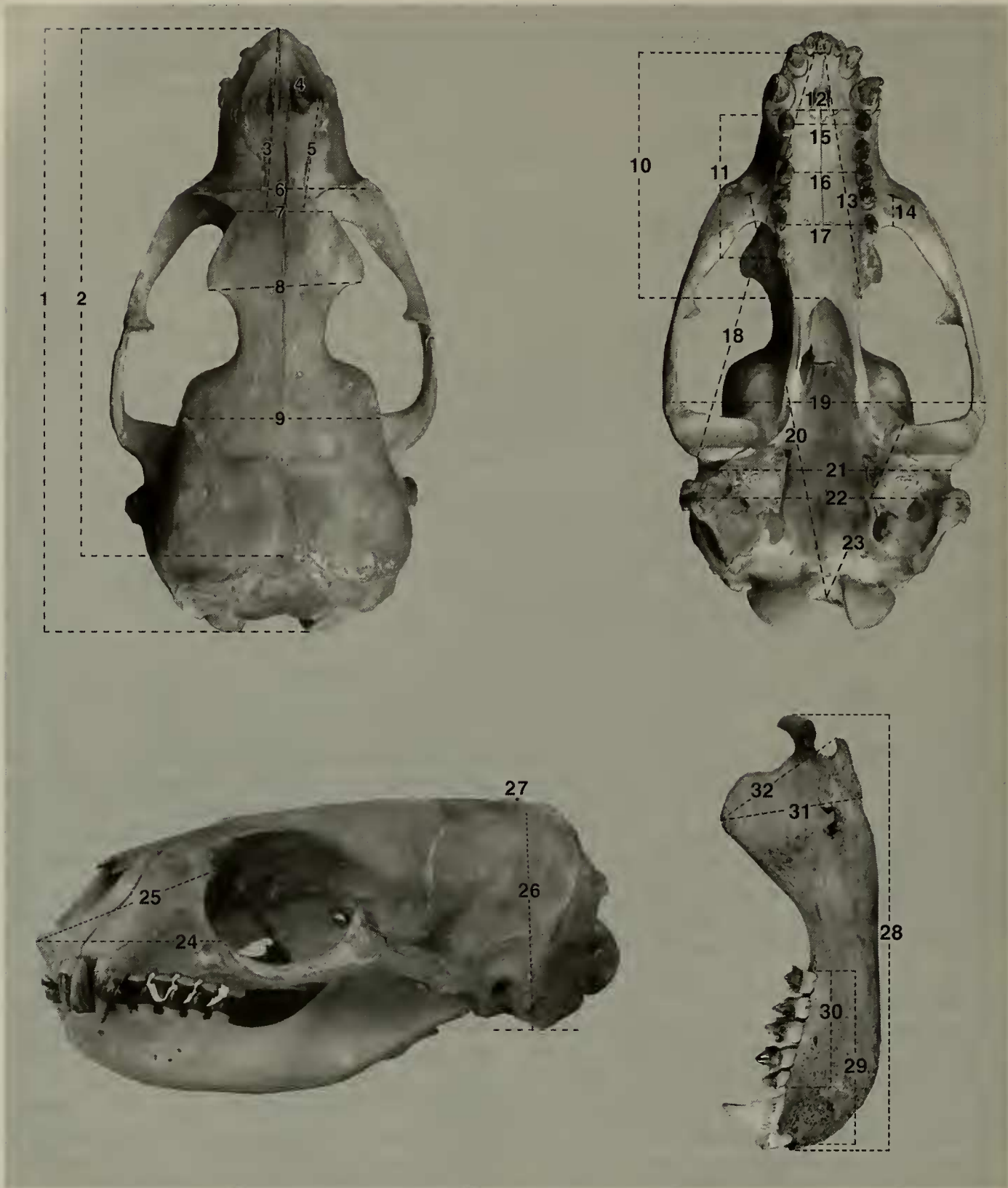
Figure 1: Diagram of a South African fur seal skull (PEM554) indicating individual measurements taken. Measurements are defined in Table 1.

(Arnould and Warneke, 2002).

Currently, examination of canine tooth structure is the most precise method of age determination in untagged pinnipeds; however, pulp cavity ring counts are not without error. In principle, other seal teeth such as postcanines, can be aged using growth ring counts in the pulp cavity up to the point where the pulp cavity closes up. For recent assessments of the reliability of this method see Arnbom et al., (1992), McCann (1993) and Oosthuizen (1997).
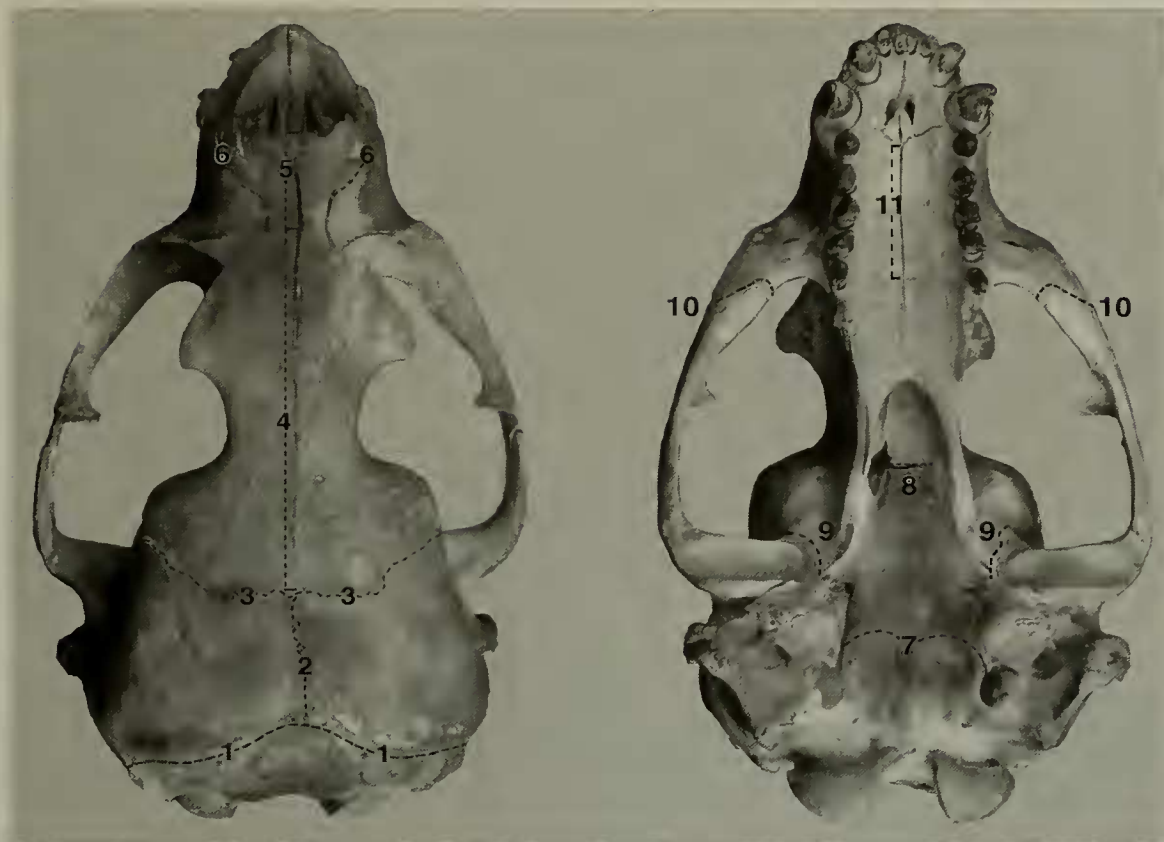
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Figure 2: Diagram of a South African fur seal skull (PEM554) showing the position of sutures examined in this study. 1. Occipito-parietal; 2. interparietal; 3. coronal; 4. interfrontal; 5. internasal; 6. premaxillary-maxillary; 7. basioccipito-basisphenoid; 8. basisphenoid-presphenoid; 9. squamosal-parietal; 10. squamosal-jugal; 11. maxillary.

Classification of growth patterns

In the present study, neural and somatic growth patterns were distinguished as follows: [(mean skull measurement for adults ≥ 12 y − mean skull measurement for subadults at 7 y) x 100%]/(mean skull measurement for subadults at 7 y). Where the percent increase in variable size was < 6%, growth was classified as neural, i.e., most growth was completed as subadults. Where percent increase was ≥ 6%, growth was classified as somatic, i.e., growth continued to increase in adults. Percentage increase for each variable is given in Table 3.

Table 2: The age distribution of Cape Fur Seals

Age group	Age (y)	Frequency	Percentage
Yearling	1	2	3.2
Subadult	2	2	3.2
	3	2	3.2
	4	8	12.7
	5	4	6.3
	6	4	6.3
	7	12	19.0
Adult	8	7	11.1
	9	5	7.9
	10	5	7.9
	≥ 12	12	19.0
Total		63	100

Pages 214-218 comprise Table 3

Summary statistics for dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull variables according to age (y) and age group. Data presented as mean skull variable in mm ± S.E., followed by coefficient of variation in round brackets, and skull variable expressed as a percentage of skull length. Maximum value of each variable (males of unknown-age), and classification of growth pattern, are also presented.

Age group	Age (y)	n	D1	D2	D3	D4	D5	D6	D7	D8	D9
Yearling	1	2	159.7 ± 2.6 (2.3)	144.8 ± 2.4 (2.3) 90.7%	54.1 ± 1.0 (2.6) 33.9%	20.3 ± 0.1 (0.7) 12.7%	25.1 ± 1.6 (8.8) 15.7%	40.8 ± 0.1 (0.3) 25.6%	21.6 ± 0.3 (1.6) 13.5%	38.2 ± 0.4 (1.5) 23.9%	78.0 ± 0.4 (0.6) 48.8%
Subadult	2	2	174.5 ± 7.2 (5.8)	148.7 ± 2.1 (2.0) 85.2%	56.3 ± 2.6 (6.4) 32.2%	17.9 ± 0.4 (3.2) 10.3%	25.7 ± 0.7 (3.9) 14.7%	45.0 ± 3.8 (11.8) 25.8%	22.1 ± 1.3 (8.0) 12.6%	37.8 ± 1.9 (7.1) 21.7%	78.7 ± 1.3 (2.2) 45.1%
	3	2	196.2 ± 1.8 (1.3)	162.8 ± 1.9 (1.7) 83.0%	64.9 ± 1.9 (4.1) 33.1%	21.5 ± 1.0 (6.6) 11.0%	33.1 ± 1.9 (8.1) 16.9%	48.6 ± 0.3 (0.7) 24.8%	24.7 ± 0.9 (5.1) 12.6%	39.5 [1]	81.7 ± 4.0 (6.8) 41.6%
	4	8	205.2 ± 4.7 (6.4)	173.6 ± 4.0 (6.6) 84.6%	71.1 ± 1.8 (7.1) 34.7%	22.8 ± 0.3 (4.2) 11.1%	34.1 ± 1.3 [6] (9.4) 16.8%	54.6 ± 1.3 (6.7) 26.6%	29.5 ± 0.8 (8.0) 14.4%	45.6 ± 1.6 (10.2) 22.2%	81.7 ± 1.1 (3.7) 39.8%
	5	4	217.0 ± 4.3 (4.0)	183.5 ± 3.4 (3.7) 84.6%	75.7 ± 1.8 (4.8) 34.9%	24.2 ± 0.5 (4.4) 11.1%	37.2 ± 0.8 (4.5) 17.1%	57.3 ± 2.3 (8.0) 26.4%	31.0 ± 1.1 (7.1) 14.3%	46.7 ± 2.0 (8.4) 21.5%	82.2 ± 1.6 (3.9) 37.9%
	6	4	220.6 ± 3.4 (3.1)	187.6 ± 4.4 (4.7) 85.0%	76.1 ± 0.7 [3] (1.6) 35.0%	23.6 ± 1.5 (12.9) 10.7%	39.0 ± 2.7 (13.9) 17.7%	59.9 ± 0.5 (1.6) 27.1%	31.2 ± 0.7 (4.6) 14.1%	46.3 ± 1.3 (5.6) 21.0%	83.7 ± 1.7 (4.0) 37.9%
	7	12	230.6 ± 2.1 (3.2)	197.8 ± 1.9 [11] (3.2) 85.5%	81.3 ± 1.5 (6.5) 35.3%	25.0 ± 0.6 [11] (7.8) 10.8%	40.1 ± 0.6 (5.1) 17.4%	63.6 ± 1.0 (5.6) 27.6%	33.9 ± 0.7 (6.9) 14.7%	52.5 ± 1.2 [11] (7.7) 22.7%	84.1 ± 0.8 (3.3) 36.4%
	2–7	32	215.7 ± 3.2 (8.3)	183.0 ± 2.9 [31] (9.0) 90.9%	74.8 ± 1.5 [31] (11.1) 34.7%	23.4 ± 0.4 [31] (10.4) 10.9%	37.0 ± 0.9 [30] (13.0) 17.1%	58.0 ± 1.2 (11.3) 26.9%	30.8 ± 0.7 (12.8) 14.3%	47.6 ± 1.0 [30] (12.0) 22.1%	82.7 ± 0.6 (3.9) 38.3%
Adult	8	7	236.8 ± 4.5 (5.0)	206.9 ± 5.6 (7.1) 87.4%	83.6 ± 2.3 (7.2) 35.3%	26.5 ± 0.9 [6] (8.7) 11.2%	41.6 ± 1.7 [6] (9.9) 17.6%	66.0 ± 1.5 (6.0) 27.9%	36.5 ± 1.2 (8.5) 15.4%	53.6 ± 0.4 [5] (1.8) 22.8%	84.6 ± 2.0 (6.3) 35.7%
	9	5	242.2 ± 1.6 (1.5)	206.5 ± 5.3 [4] (5.1) 85.1%	84.3 ± 1.9 [4] (4.6) 34.8	28.2 ± 1.2 (9.4) 11.6%	40.5 ± 2.0 [4] (9.9) 16.7%	67.2 ± 1.5 [4] (4.3) 27.7%	38.4 ± 1.9 [4] (9.9) 15.8%	56.5 ± 2.8 [3] (8.6) 23.2%	83.1 ± 1.3 (3.0) 34.3%
	10	5	248.2 ± 4.7 (4.2)	220.1 ± 6.1 (6.1) 88.7%	89.9 ± 2.5 (6.3) 36.2%	29.0 ± 1.0 (8.1) 11.7%	44.3 ± 2.1 (10.7) 17.9%	68.7 ± 3.2 (10.3) 27.7%	38.6 ± 0.7 [4] (3.6) 15.3%	57.3 ± 1.9 (7.5) 23.1%	84.2 ± 0.9 (2.3) 33.9%
	8–10	17	241.7 ± 2.5 (4.3)	210.9 ± 3.5 [16] (6.7) 87.2%	85.7 ± 1.4 [16] (6.9) 35.5%	27.8 ± 0.6 [16] (9.1) 11.5	42.2 ± 1.1 [15] (10.2) 17.5%	67.2 ± 1.2 [16] (7.1) 27.8%	37.6 ± 0.8 [15] (7.8) 15.5%	55.7 ± 1.0 [13] (6.6) 23.0%	84.0 ± 0.9 (4.5) 34.8%
	≥ 12	12	249.9 ± 4.1 (5.7)	225.3 ± 5.0 [11] (7.3) 90.1%	92.4 ± 2.2 (8.1) 37.0%	29.6 ± 0.8 (9.0) 11.9%	47.0 ± 1.4 (10.1) 18.8%	69.1 ± 1.8 [10] (8.4) 27.9%	38.0 ± 1.2 [10] (9.6) 15.2%	58.0 ± 2.1 (12.4) 23.2%	84.0 ± 1.3 (5.2) 33.6%
Total		63	63	60	61	61	59	60	59	57	63
Mean for males ≥ 200 cm			259.2 ± 7.0	234.8 ± 9.4	97.4 ± 4.7	30.6 ± 1.1	50.2 ± 2.9	72.3 ± 4.0 [3]	38.4 ± 0.5	62.8 ± 2.3	85.2 ± 0.9 [3]
Max. value of largest male			275.4	254.4	108.9	33.8	57.6	77.0	42.8	69.1	90.0
Growth pattern			Somatic, 8%	Somatic, 14%	Somatic, 14%	Somatic, 18%	Somatic, 17%	Somatic, 9%	Somatic, 12%	Somatic, 10%	Neural, 0%
Evidence of a SGS			No	10 y (strong)	10 y (weak)	No	(see text)	No	No	7 y (weak)	No

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Age group	Age (y)	n	P10	P11	P12	P13	P14	P15	P16
Yearling	1	2	64.3 ± 0.7 (1.4) 40.2%	40.5 [1]	33.8 ± 1.2 (4.8) 21.1%	73.0 ± 0.5 (1.0) 45.7%	12.9 ± 0.5 (5.5) 8.1%	14.1 ± 0.7 (6.5) 8.8%	18.4 ± 0.5 (3.8) 11.5%
Subadult	2	2	66.2 ± 3.0 (6.4) 37.9%	43.2 ± 0.3 (0.8) 24.7%	32.5 ± 1.6 (6.8) 18.6%	77.7 ± 1.2 (2.1) 44.5%	11.3 ± 0.3 (3.8) 6.5%	13.0 ± 0.4 (3.8) 7.4%	16.7 ± 0.3 (2.5) 9.6%
	3	2	82.3 ± 2.8 (4.8) 42.0%	62.1 ± 0.7 (1.5) 31.6%	35.2 ± 0.8 (3.0) 17.9%	89.3 ± 0.1 (0.2) 45.5%	12.4 ± 0.3 (3.4) 6.3%	16.3 ± 0.2 (1.7) 8.3%	19.6 [1]
	4	8	87.9 ± 2.5 (8.1) 42.8%	49.8 ± 0.4 (2.5) 24.3%	39.6 ± 0.8 (5.5) 19.3%	94.2 ± 2.7 (8.1) 45.9%	12.7 ± 0.3 (7.0) 6.2%	17.2 ± 0.5 (7.7) 8.4%	21.9 ± 0.6 (7.2) 10.6%
	5	4	88.6 ± 2.3 [3] (4.4) 41.6%	54.2 ± 2.4 (9.0) 25.0%	42.5 ± 1.3 (6.1) 19.6%	101.9 ± 3.2 (6.2) 47.0%	14.5 ± 0.7 (9.5) 6.7%	20.7 ± 1.2 [3] (9.8) 9.4%	23.8 ± 1.1 [3] (7.9) 10.8%
	6	4	94.1 ± 1.1 (2.7) 42.3%	54.9 ± 0.8 (3.3) 24.7%	43.0 ± 0.7 (3.4) 19.6%	103.9 ± 1.4 (3.0) 47.0%	14.1 ± 0.6 (8.8) 6.4%	19.6 ± 0.4 (4.2) 8.9%	23.4 ± 0.6 (6.1) 10.5%
	7	12	97.8 ± 1.7 (6.0) 42.4%	57.2 ± 0.8 (4.8) 24.8%	45.9 ± 0.5 [11] (3.3) 19.8%	110.6 ± 1.3 (4.0) 48.0%	13.8 ± 0.4 (10.4) 6.0%	20.7 ± 1.2 [8] (16.0) 8.9%	25.0 ± 0.4 [8] (4.5) 10.7%
	2–7	32	90.9 ± 1.7 [31] (10.6) 42.2%	54.2 ± 0.9 (9.3) 25.1%	41.9 ± 0.8 [31] (10.3) 19.5%	101.3 ± 1.9 (10.6) 46.9	13.4 ± 0.3 (10.6) 6.2%	18.6 ± 0.6 [27] (16.2) 8.7%	22.8 ± 0.5 [26] (11.5) 10.6%
Adult	8	7	99.6 ± 2.5 (6.6) 42.1%	57.7 ± 1.8 (8.4) 24.4%	47.9 ± 1.3 (7.2) 20.2%	112.0 ± 2.6 (6.0) 47.3%	14.4 ± 0.5 (9.7) 6.1%	23.4 ± 0.8 [6] (8.8) 9.9%	26.3 ± 0.9 [6] (8.3) 11.1%
	9	5	105.6 ± 0.7 (1.5) 43.6%	60.2 ± 1.2 (4.4) 24.9%	46.6 ± 0.8 (3.7) 19.2%	115.0 ± 0.9 [4] (1.5) 47.3%	14.4 ± 0.7 (11.0) 5.9%	22.6 ± 0.7 [4] (6.5) 9.3%	25.0 ± 0.9 [4] (7.1) 10.3%
	10	5	109.3 ± 3.7 (7.6) 44.0%	59.3 ± 1.2 (4.7) 23.9%	51.1 ± 2.8 (12.2) 20.6%	117.2 ± 1.9 (3.6) 47.2%	16.0 ± 1.1 (14.9) 6.4%	26.7 ± 1.1 [4] (8.1) 10.6%	27.0 ± 1.8 (14.8) 10.9%
	8–10	17	104.2 ± 1.8 (6.9) 43.1%	58.9 ± 0.9 (6.3) 24.4%	48.4 ± 1.0 (8.9) 20.0%	114.4 ± 1.3 [16] (4.7) 47.3%	14.8 ± 0.4 (12.3) 6.1%	24.1 ± 0.7 [14] (10.3) 9.9%	26.2 ± 0.7 [15] (10.6) 10.8%
	≥ 12	12	106.3 ± 2.0 (6.3) 42.0%	62.0 ± 1.6 (8.6) 24.5%	54.1 ± 1.1 (6.8) 21.4%	118.4 ± 2.4 (6.8) 46.7%	17.2 ± 0.4 (7.7) 6.8%	28.0 ± 0.8 [11] (11.3) 11.0%	30.0 ± 0.8 [11] (8.5) 11.8%
Total		63	62	62	62	62	63	54	54
Mean for males ≥ 200 cm			112.8 ± 4.4	60.5 ± 2.1	53.7 ± 3.3	123.7 ± 4.1	17.4 ± 1.0	28.7 ± 2.5	28.9 ± 1.4
Max. value in largest male			123.0	70.5	62.2	134.6	20.0	35.4	32.7
Growth pattern			Somatic, 9%	Somatic, 8%	Somatic, 18%	Somatic, 7%	Somatic, 25%	Somatic, 35%	Somatic, 20%
Evidence of a SGS			No	No	(see text)	No	No	No	No

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Age group	Age (y)	n	P17	P18	P19	P20	P21	P22	P23
Yearling	1	2	20.8 ± 0.1 (0.3) 13.0%	111.1 ± 0.3 (0.3) 69.6%	86.6 ± 0.5 (0.8) 54.2%	109.3 ± 2.2 (2.8) 68.5%	77.3 ± 2.0 (3.7) 48.4%	74.8 ± 2.1 (4.0) 46.9%	59.6 ± 0.9 (2.0) 37.3%
Subadult	2	2	20.7 ± 0.7 (4.8) 11.9%	122.4 ± 3.4 (3.9) 70.2%	92.6 ± 3.0 (4.5) 53.1%	120.0 ± 5.7 (6.7) 68.9%	77.8 ± 1.5 (2.6) 44.6%	82.0 ± 3.2 (5.4) 47.0%	62.6 ± 4.1 (9.2) 35.9%
	3	2	25.0 ± 1.6 (8.8) 12.7%	141.0 ± 1.3 (1.3) 71.9%	103.8 ± 1.7 (2.2) 52.9%	133.0 ± 0.4 (0.4) 67.8%	87.3 ± 0.7 (1.0) 44.5%	93.9 ± 0.7 (1.0) 47.8%	66.5 ± 0.7 (1.4) 33.9%
	4	8	26.0 ± 1.1 (12.3) 12.7%	150.0 ± 4.1 (7.8) 73.1%	111.0 ± 2.7 (6.8) 54.1%	139.8 ± 3.2 (6.5) 68.1%	93.6 ± 2.4 (7.4) 45.6%	100.9 ± 2.8 (7.9) 49.2%	69.8 ± 1.2 (5.0) 34.0%
	5	4	30.1 ± 1.7 (11.2) 13.9%	162.4 ± 4.7 [3] (5.0) 74.1%	121.9 ± 3.6 (5.9) 56.2%	148.3 ± 2.6 (3.5) 68.4%	104.0 ± 2.3 (4.4) 47.9%	109.8 ± 3.5 (6.3) 50.6%	74.6 ± 0.9 (2.5) 34.4%
	6	4	29.2 ± 1.2 (9.1) 12.9%	162.1 ± 1.7 [4] (2.1) 74.2%	121.0 ± 3.2 (6.0) 54.5%	150.2 ± 1.3 (1.9) 68.0%	102.6 ± 0.4 (0.8) 46.5%	111.5 ± 1.6 (3.2) 50.3%	73.8 ± 0.4 (1.2) 33.6%
	7	12	30.5 ± 0.7 [11] (7.6) 13.2%	173.2 ± 1.8 [10] (3.3) 74.9%	125.7 ± 2.1 (5.7) 54.5%	157.5 ± 1.4 (3.0) 68.3%	107.5 ± 1.3 (4.3) 46.6%	119.3 ± 1.8 (5.1) 51.7%	76.2 ± 0.7 (3.2) 33.0%
	2–7	32	28.2 ± 0.7 [31] (13.4) 13.0%	158.4 ± 3.0 [28] (10.3) 73.8%	117.6 ± 2.0 (9.8) 54.5%	147.2 ± 2.1 (8.2) 68.2%	99.9 ± 1.7 (9.8) 46.3%	108.7 ± 2.1 (11.3) 50.3%	72.7 ± 0.8 (6.5) 33.7%
Adult	8	7	32.6 ± 0.9 (7.3) 13.8%	178.5 ± 4.2 (6.3) 75.4%	135.1 ± 3.3 (6.4) 57.1%	161.0 ± 3.4 [6] (5.6) 68.0%	111.8 ± 2.5 (5.4) 47.4%	124.4 ± 2.7 (5.8) 52.5%	77.4 ± 1.2 (4.1) 32.7%
	9	5	29.8 ± 1.1 (8.1) 12.3%	184.3 ± 2.0 [4] (2.1) 75.9%	137.1 ± 1.8 (2.9) 56.6%	164.6 ± 0.7 (1.0) 68.0%	112.0 ± 1.5 (3.0) 46.3%	125.0 ± 3.5 [4] (5.5) 51.9%	76.7 ± 1.0 [4] (2.5) 31.9%
	10	5	35.7 ± 0.3 [4] (1.9) 14.1%	189.0 ± 3.4 (4.1) 76.2%	141.8 ± 2.9 (4.6) 57.1%	173.3 ± 2.7 [4] (3.1) 68.7%	115.5 ± 2.9 (5.7) 46.6%	134.3 ± 4.4 (7.4) 54.1%	78.6 ± 2.6 (7.3) 31.7%
	8–10	17	32.5 ± 0.8 [16] (9.3) 13.4%	183.2 ± 2.4 [16] (5.2) 75.8%	137.7 ± 1.7 (5.2) 57.0%	165.2 ± 2.0 [15] (4.8) 68.2%	113.0 ± 1.4 (4.8) 46.8%	127.6 ± 2.2 [16] (6.9) 52.9%	77.6 ± 0.9 [16] (4.8) 32.0%
	≥ 12	12	35.8 ± 0.6 (6.5) 14.1%	195.3 ± 2.1 [11] (3.4) 76.0%	150.6 ± 2.1 (4.7) 59.5%	173.6 ± 1.8 (3.7) 68.5%	121.0 ± 1.6 (4.3) 47.8%	139.4 ± 2.2 [11] (5.0) 55.3%	80.4 ± 0.9 [11] (3.5) 31.8%
Total		63	61	57	63	61	63	61	61
Mean for males ≥ 200 cm			36.5 ± 1.6	197.0 ± 6.3	140.0 ± 2.0	174.8 ± 4.9	120.2 ± 2.7	139.7 ± 4.5	84.2 ± 1.8
Max. value in largest male			40.9	211.6	158.9	183.4	126.1	149.7	87.4
Growth pattern			Somatic, 17%	Somatic, 13%	Somatic, 20%	Somatic, 10%	Somatic, 13%	Somatic, 17%	Neural, 5%
Evidence of a SGS			(see text)	No	No	No	No	10 y (strong)	No

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Age group	Age (y)	n	L24	L25	L26	L27
Yearling	1	2	45.7 ± 2.5 (7.6) 28.6%	48.3 ± 0.4 (1.2) 30.3%	73.1 [1]	0.0
Subadult	2	2	42.2 ± 2.7 (9.0) 24.2%	52.2 ± 1.7 (4.5) 29.9%	72.3 ± 0.9	0.0 [1]
	3	2	57.1 ± 3.6 (8.9) 29.1%	59.1 ± 0.3 (6.7) 30.1%	– [0]	0.0
	4	8	61.4 ± 2.7 (12.4) 29.9%	64.3 ± 2.5 (11.2) 31.3%	77.6 ± 0.6 [4]	0.07 ± 0.07 [7]
	5	4	63.1 ± 1.2 (3.9) 29.1%	69.3 ± 1.8 (5.2) 31.9%	86.0 ± 2.1 [3]	0.0 [2]
	6	4	64.5 ± 1.8 (6.2) 29.8%	71.9 ± 1.4 (4.3) 32.5%	86.5 ± 0.8 [3]	0.7 ± 0.5 [4]
	7	12	69.4 ± 1.1 (5.5) 30.1%	75.0 ± 1.0 (4.8) 32.5%	94.2 ± 1.5 [9]	4.5 ± 1.2 [8]
	2–7	32	63.6 ± 1.4 (12.8) 29.5%	68.9 ± 1.4 (11.5) 31.9%	86.7 ± 1.8 [21]	1.6 ± 0.6 [24]
Adult	8	7	71.6 ± 1.4 (5.2) 30.3%	77.9 ± 1.5 (5.0) 32.9%	100.1 ± 3.3	5.4 ± 0.7 [4]
	9	5	71.8 ± 0.7 (2.2) 29.6%	78.8 ± 1.3 [4] (3.3) 32.5%	101.8 ± 5.3	6.0 ± 1.6 [3]
	10	5	74.0 ± 1.7 (5.3) 29.8%	82.1 ± 2.0 (5.5) 33.1%	108.0 ± 6.8	9.2 ± 1.3
	8–10	17	72.4 ± 0.8 (4.5) 29.9%	79.4 ± 1.0 [16] (5.1) 32.9%	103.5 ± 2.8	7.1 ± 0.8 [12]
	≥ 12	12	78.2 ± 1.1 (4.6) 30.9%	85.6 ± 1.1 (4.4) 33.8%	115.5 ± 1.0 [11]	8.2 ± 0.8 [9]
Total		63	63	62	50	47
Mean for males ≥ 200 cm			80.8 ± 2.9	89.0 ± 3.2	116.4 ± 4.8	6.5 ± 1.2
Max. value in largest male			88.3	96.6	126.2	12.0
Growth pattern			Somatic, 13%	Somatic, 19%	Somatic, 23%	Somatic, 82%
Evidence of a SGS			No	No	10 y (weak)	(see text)

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Age group	Age (y)	n	M28	M29	M30	M31	M32
Yearling	1	2	98.9 ± 0.1 (0.1) 62.9%	46.8 ± 1.5 (4.5) 28.8%	37.4 [1]	25.9 [1]	28.3 [1]
Subadult	2	2	114.8 ± 9.1 (11.2) 65.8%	50.9 ± 1.0 (2.8) 29.2%	35.9 ± 0.1 (0.4) 20.6%	29.1 ± 3.3 (15.8) 16.7%	32.0 ± 1.4 (6.0) 18.3%
	3	2	126.0 ± 1.2 (1.3) 64.2%	54.3 ± 1.2 (3.1) 28.5%	39.4 ± 0.8 (2.7) 20.6%	35.6 ± 2.4 (9.3) 17.1%	38.4 ± 1.8 (6.6) 18.8%
	4	8	136.5 ± 3.8 (7.9) 66.5%	59.3 ± 2.4 (11.6) 28.9%	39.4 ± 1.1 [6] (6.7) 19.5%	38.4 ± 1.9 [7] (12.8) 18.7%	40.5 ± 2.1 [7] (13.9) 18.7%
	5	4	147.2 ± 4.8 (6.5) 67.8%	61.3 ± 1.0 [3] (2.9) 28.8%	42.5 ± 0.8 (4.0) 19.6%	41.7 ± 2.1 (9.9) 19.2%	45.7 ± 1.4 (6.1) 21.1%
	6	4	149.7 ± 1.9 (2.9) 68.0%	61.3 ± 1.4 [3] (4.6) 27.6%	43.5 ± 0.7 (3.9) 19.6%	44.2 ± 1.5 (7.7) 20.4%	46.2 ± 1.3 (6.5) 21.2%
	7	12	159.6 ± 1.7 (3.7) 68.7%	67.5 ± 0.6 (3.2) 29.0%	45.4 ± 0.4 (2.9) 19.5%	48.2 ± 0.9 (6.5) 20.8%	49.3 ± 0.9 (6.3) 21.3%
	2–7	32	146.3 ± 2.7 (10.5) 67.6%	62.1 ± 1.1 [30] (10.2) 28.9%	42.5 ± 0.6 [30] (8.0) 19.6%	42.6 ± 1.2 [31] (15.6) 19.7%	44.7 ± 1.1 [31] (13.7) 20.7%
Adult	8	7	168.1 ± 3.5 [6] (5.1) 70.5%	70.0 ± 1.0 (3.7) 29.6%	46.7 ± 0.8 (4.3) 19.7%	54.2 ± 1.9 (9.5) 22.9%	54.4 ± 1.9 (9.2) 23.0%
	9	5	168.8 ± 1.1 (1.4) 69.7%	67.4 ± 0.6 (1.9) 27.8%	46.6 ± 0.7 (3.3) 19.3%	53.7 ± 2.1 (8.8) 22.2%	53.2 ± 1.4 (5.8) 22.0%
	10	5	177.0 ± 6.0 (7.6) 71.3%	69.7 ± 1.8 [4] (5.1) 28.4%	46.3 ± 1.2 (5.7) 18.6%	59.5 ± 3.8 (14.2) 24.0%	58.0 ± 3.8 [4] (13.0) 23.4%
	8–10	17	171.1 ± 2.4 [16] (5.6) 70.5%	69.1 ± 0.7 [16] (3.9) 28.7%	46.6 ± 0.5 (4.2) 19.3%	55.6 ± 1.5 (11.4) 23.0%	54.9 ± 1.3 [16] (9.5) 22.8%
	≥ 12	12	175.1 ± 3.9 (7.7) 70.2%	67.9 ± 2.0 [8] (8.4) 27.8%	46.6 ± 1.1 [11] (7.9) 18.6%	61.7 ± 2.4 (13.4) 25.0%	61.7 ± 1.9 (10.6) 24.6%
Total		63	62	56	59	61	60
Mean for males ≥ 200 cm			184.1 ± 6.1	75.4 ± 8.1	47.0 ± 1.3	62.2 ± 3.5	65.8 ± 1.6
Max. value in largest male			194.1	83.5	52.5	68.8	69.0
Growth pattern			Somatic, 10%	Neural, 0.6%	Neural, 3%	Somatic, 28%	Somatic, 25%
Evidence of a SGS			No	No	No	10 y (weak)	10 y (weak)

1999, 12.23), Microsoft Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

RESULTS

Skull measurement error

Of the 7 variables that were measured twice, measurements were reproducible at the 5% significance level (range for p-values: 1.0–0.08). Heights of sagittal crest (L27), and heights of the skull at base of mastoid (L26), were both difficult to measure reproducibly. Hence the sagittal crest (L27) and base of mastoid (L26) data needs to be interpreted with caution. All errors are quoted as standard deviations (SD) or standard errors (SE) as appropriate.

Skull morphology

The youngest animals in the sample were 10 months of age (Figure 3a; Table 3). In these individuals, the skull was c. 160 ± 2.6 (SE, n = 2) mm in length (D1) and 87 ± 0.5 (SE, n = 2) mm wide (P19). The brain case was relatively long, measuring approximately 120 mm (75% of CBL) from the most posterior end of nasals to the most posteriorly projecting point on the occipital bone, in the mid-sagittal plane. There were no signs of bony ridges or prominences. Relative to CBL, the face and mandible were short (Figure 3a). Milk dentition had not been completely replaced by permanent teeth in animal AP4999. It was clear that the deciduous canines persist in at least some animals until their tenth month.

In adults 10 y of age, the skull was rugose, with heavy bony deposits (Figure 3b; Table 3). Mean length (D1) and breadth (P19) was 248 ± 4.7 (SE, n=5) mm and 142 ± 2.9 (SE, n = 5) mm, respectively. The braincase was approximately 157 mm in length (or 63% of CBL), and a sagittal crest was always present but varied greatly in height (range 4.4–12.0 mm) or 9.2 ± 1.3 mm in height (SE, $n = 5$). The forehead was convex at the supraorbital region. Relative to CBL, the face was long, with long nasals that flared anteriorly. The ratio of nasal breadth to length was 1: 1.5. The palate was long, moderately broad and arched. The ratio of palatal breadth (P15–17) to palatal length (P10) was 1: 3–4. The maxillary shelf at the root of the zygomatic process (P14) was very short in an anterior-posterior direction (16 mm; 6% of CBL). The mandible was long with a broad coronoid process. The tooth rows were parallel, with enlarged third incisor; large canines; robust, tricuspid

postcanines (PC); and a slight diastema between upper PC 5 and 6 (Repenning et al., 1971; present study). Dental formula was (I 3/2 C 1/1 PC 6/5). In seals, the premolars and molars are similar in appearance and are collectively termed postcanines.

East Coast and West Coast animals

Available data suggested that skulls from adult males, 7–12[+] y, from Eastern Cape fur seals (mean 246.6 ± 2.5 mm (SD); range 213.7–266.8 mm; $n = 28$) were significantly smaller than skulls from adult animals inhabiting west coast waters (mean 259.4 ± 4.5 mm (SD); range 225.6–282.1 mm; $n = 12$) (at the 5% significance level two sample t-test: $t = -2.48$; P = 0.024; $df = 17$).

However, skulls from adult males, ≥ 12 y, from the Eastern Cape (mean 255.7 ± 2.6 mm (SD); range 239.9–266.6 mm; $n = 11$) were not significantly smaller than skulls classed as from adult animals from west coast waters (mean 259.4 ± 4.5 mm (SD); range 225.6–282.1 mm; $n = 12$) (at the 5% significance level for a two sample t-test: $t = -0.71$; P = 0.49; $df = 17$).

Condylobasal length (CBL) expressed in relation to standard body length (SBL)

In the cases where a seal carcass was the source of the skull material it was possible to measure skull size (CBL) and relate it to the standard body length (SBL) and both to age. Animals seem to cease growth in length at 10 y. It was found that the relative condylobasal length decreased with increasing SBL, i.e., 19.4% (yearlings), 15.5% (subadults), 13.8% (adults, 8–10 y) and 13.6% (adults ≥ 12 y) (Table 4).

Condylobasal length as an indicator of age

Condylobasal length continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). In animals 1–10 y, growth in skull length was highly positively correlated with age (y) ($r = 0.89$, $n = 51$) (Figure 4b). However, after fitting the straight-line model, the plot of the residuals versus fitted values was examined, and the straight-line model was found to be inadequate (the residuals were not scattered randomly about zero, see Weisberg, 1985, p. 23). Thus, CBL could not be used as a reliable indicator of absolute age, particularly in young and old animals (Figure 4b). The coefficient of variation in skull length for young males 1–5 y (12.3%) was considerably higher than in older males (8–10 y, 4.3%; ≥ 12 y, 5.7%) (Table 3) suggesting that young males may grow at different rates but survivors to old age fall into a narrower range of sizes. This may reflect higher mortality of smaller juveniles.

Although CBL was not an accurate indicator of
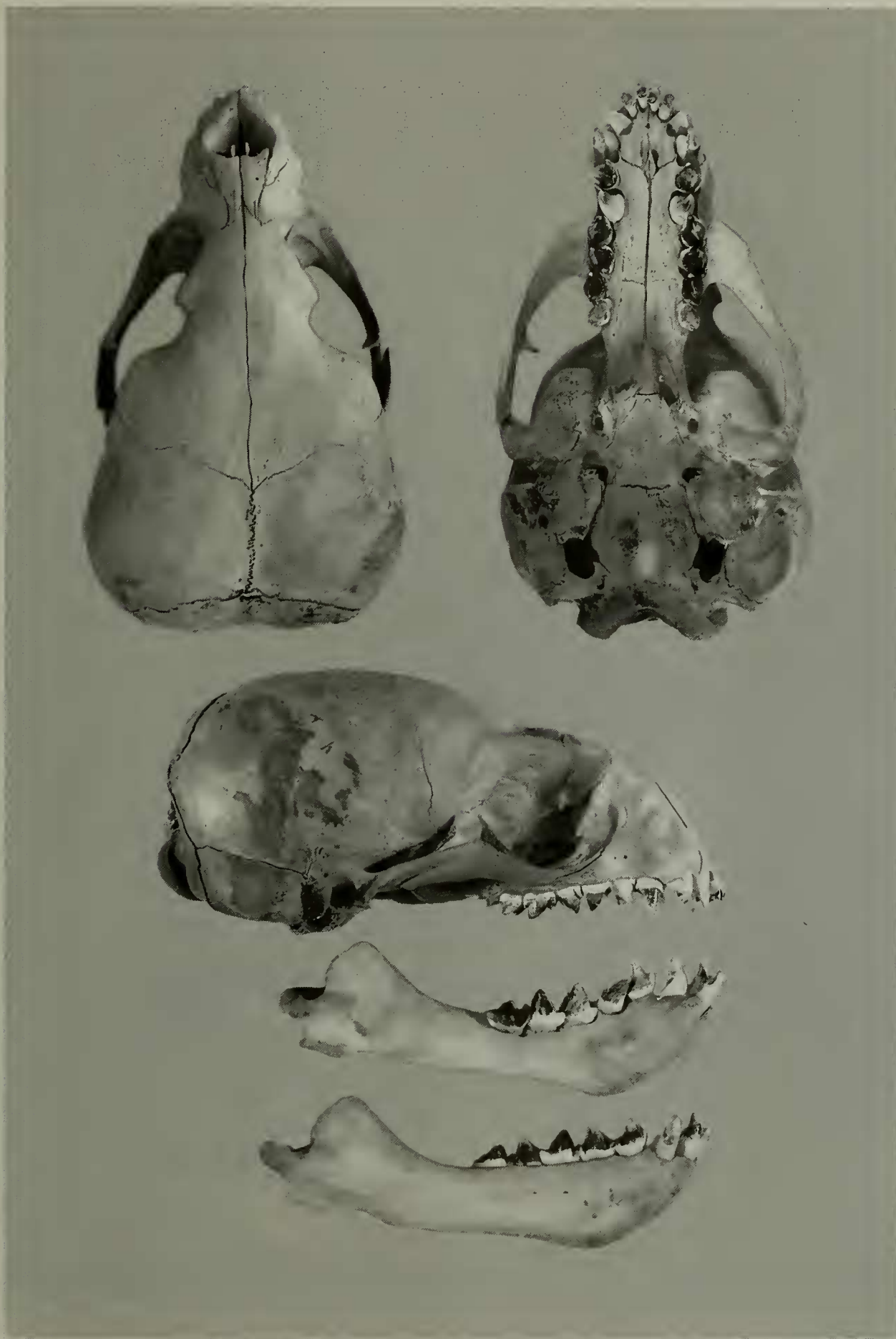
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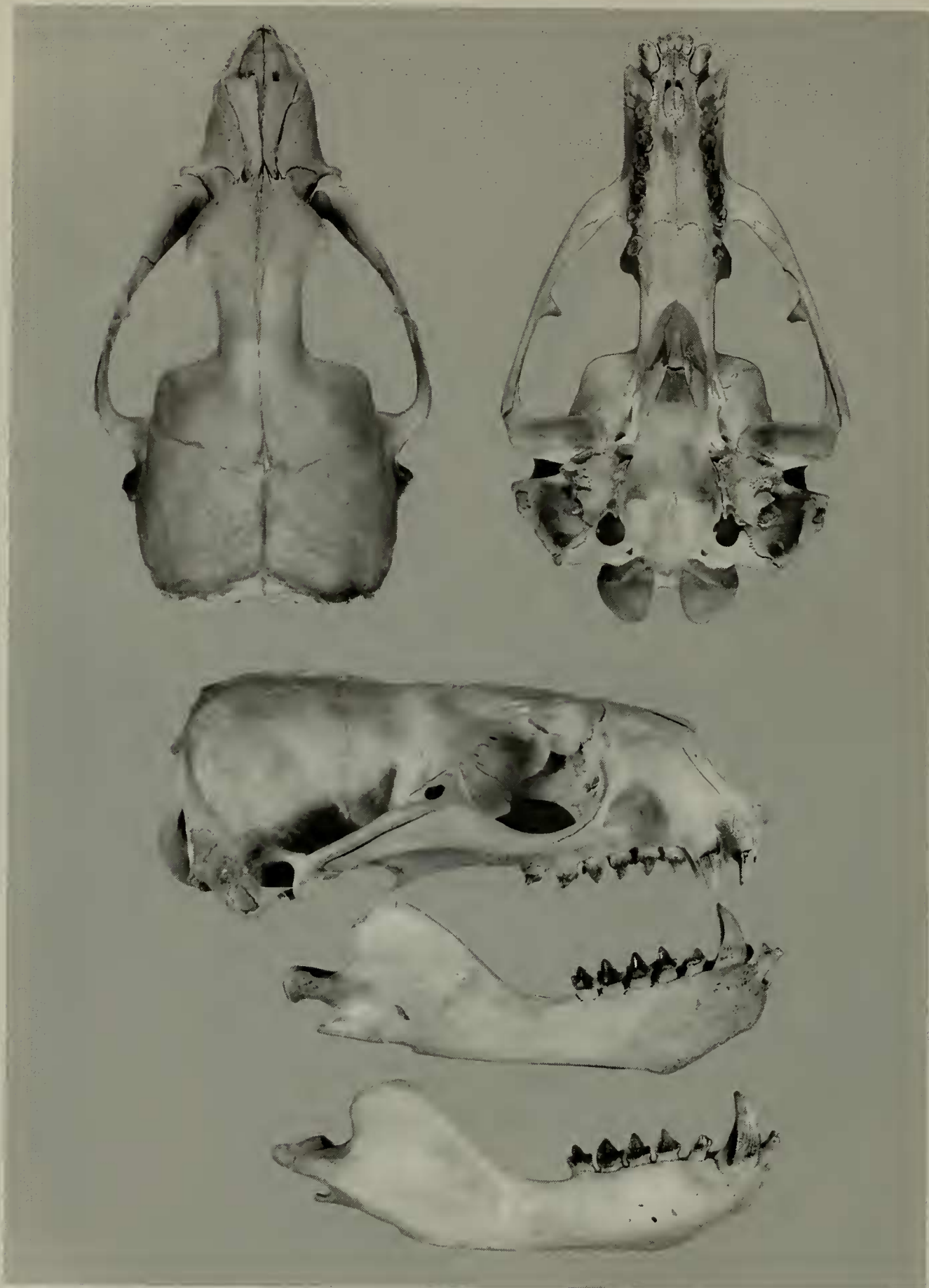Figure 3a: Size and shape of the South African fur seal skull: juvenile 10 months (AP4999).

Figure 3b: Size and shape of the South African fur seal skull: male adult 10 y (AP4992).

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Table 4: Growth in mean condylobasal length relative to mean standard body length (SBL)

Age group	Age (y)	n	Mean CBL (mm)	Mean SBL (cm)	CBL rel. to SBL
Yearling	1	2	159.7 ± 2.6	82.5 ± 2.5	19.4%
Subadult	2	2	174.5 ± 7.2	94.5 ± 4.5	18.5%
	3	2	196.2 ± 1.8	121.0 ± 3.0	16.2%
	4	8	205.2 ± 4.7	126.0 ± 5.2	16.3%
	5	4	219.3 ± 5.1 [3]	141.0 ± 3.8 [3]	15.6% [3]
	6	4	220.6 ± 3.4	149.0 ± 1.7	14.8%
	7	12	232.0 ± 2.5 [9]	159.0 ± 3.4 [9]	14.6% [9]
	2–7	32	214.7 ± 3.6 [28]	138.9 ± 4.1 [28]	15.5% [28]
Adult	8	7	238.8 ± 6.0 [5]	170.4 ± 7.6 [5]	14.0% [5]
	9	5	242.7 ± 2.0 [4]	170.8 ± 2.3 [4]	14.2% [4]
	10	5	248.2 ± 4.7	187.4 ± 6.5	13.2%
	8–10	17	243.3 ± 2.8 [14]	176.6 ± 4.0 [14]	13.8% [14]
	≥ 12	12	250.4 ± 4.5 [11]	183.7 ± 5.8 [11]	13.6% [11]
Total		63	55	55	55

absolute age, it was a 'rough estimator' of age group. When skull length (CBL) is known, the following linear discriminant functions can be used to categorise each observation into one of two age groups–adult or subadult:

$$Log(y_1) = -98.43 + 0.91 \times Log(CBL)$$
$$Log(y_2) = -129.06 + 1.05 \times Log(CBL)$$

where CBL is the skull length (mm); subscript 1 = subadult; and subscript 2 = adult. The seal is classified into the age group associated with the linear discriminant function which results in the minimum value. Of the 61 observations in this study 85% could be correctly classified using this method (Table 5).

Condylobasal length as an indicator of SBL

Skull length (CBL) was highly, positively correlated with SBL ($r = 0.93$, $n = 74$; Figure 4a). When CBL is known, the following equation (linear least squares fit; log-transformed data) can be used as an 'estimator' of SBL:

$$Log(y) = -4.11 + 1.69 \times Log(CBL)$$

which may equivalently be written as $SBL = e^{-4.11} \times CBL^{1.69}$ or $0.01641 \times CBL^{1.69}$, where the standard error (SE) of the intercept is 0.28 and the SE of the slope is 0.05 ($n = 74$).

Suture index as an indicator of age

The sequence of suture closure according to age (y) and age group is shown in Table 6. Sutures *i–xi* showed signs of partial closure at different times, and the time taken to reach full closure was different for each suture. The cranial sutures (basioccipito-basisphenoid, coronal, occipito-parietal and interparietal) were the first to partially close. The squamosal-jugal, squamosal-parietal, maxillary, premaxillary-maxillary, and interfrontal were the last to show signs of partial closure (order of partial closure unknown), with the basisphenoid-presphenoid and internasal remaining fully open in all specimens examined.

The exact sequence of full closure for all 11 sutures could not be established because animals of known-age, ≥ 12 y, were not available (The definitive ages of such old individuals can only be determined from tagging). However, the basioccipito-basisphenoid and occipito-parietal were the first sutures to fully

close in animals 3 and 4 y, respectively; followed by the interparietal in some animals ≥ 7 y; and then the coronal or squamosal-jugal in animals ≥ 12 y.

In animals 1–10 y, suture age was highly positively correlated with age ($r = 0.81, p \leq 0.001, n = 38$) (Figure 5c). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate.

Furthermore, linear discriminant function analysis could not be used satisfactorily to categorise each observation into age groups, i.e., of the 46 animals examined, all subadults ($n = 26$) were correctly classified; however, seven (35%) of the 20 adults were incorrectly classified as subadults.

Suture age was highly positively correlated with SBL ($r = 0.89, p < 0.001, n = 63$) (Figure 5a). Further information on suture age as an indicator of physiological maturity is presented elsewhere (Stewardson 2001).

Bivariate allometric regression

Regression statistics for skull measurements for sub-adults (y1) and adults (y2) are given in Appendices 2, 3 & 4. The log-transformations of the parameters (D1–M32) are regressed on Log(SBL), Log(CBL) and Log(age) respectively. Overall, correlation coefficients were moderately to strongly positive, i.e., most points on the scatter plot approximate a straight line with positive slope, $r \geq 0.70$. Exceptions included breadth of brain case (D9) on SBL, CBL and age (y) ($r = 0.3$–0.4); length of upper PC row on age (y) ($r = 0.59$), and breadth of zygomatic root of maxilla on age (y) ($r = 0.57$). SBL was strongly positively correlated with age (y) ($r = 0.87$). Although correlation coefficients indicate that linearity was reasonably well approximated for most variables after log-log transformations of the data, a linear relation (Log y vs. Log x) did not necessarily best describe the relationship. A larger data set would be needed to find an optimum relationship using more complex models such as the Logistic growth curve, which has an asymptotic maximum.

Growth of skull variables according to region

Most variables within a given region of a skull were significantly positively correlated with each other, $r \geq 0.70$ (Appendix 4.5). Exceptions were: (i) breadth of palate at PC 5 (P17) with length of upper PC row (P11) ($r < 0.7$; significant at p < 0.01); and (ii) breadth of brain case (D9) with height of sagittal crest (L27) ($r = 0.25$; not significant).

Neurocranium region (D9, L27)

Breadth of brain case (D9) followed a neural growth pattern, with most growth completed by 6 y (84 mm) (Figure 6). Overall growth scaled with negative slope ($b = 0.17$) relative to CBL. In yearlings, the brain case was proportionally long, i.e., 75% of CBL in yearlings, and 63% of CBL at 10 y. Growth in length of the brain case (31% at 10 y relative to yearlings abbreviated to RTY) was much greater than growth in breadth (8% at 10 y, RTY). The ratio of breadth to length increased from 1: 1.5 (yearlings) to 1: 1.9 y (10 y).

Height of sagittal crest (L27) appeared to follow a somatic growth pattern; however, there was great variation among individuals of similar age. The crest was absent in juveniles and young subadults. Evidence of crest formation was apparent in one 4 y old ($n = 7$), two 6 y olds ($n = 4$), eight 7 y olds ($n = 8$), and all males ≥ 8 y. Maximum crest height was 11–12 mm ($n = 4$). There was some evidence of a very slight secondary growth spurt in some males at c. 10 y, but sample size was too small to confirm this observation.

Basicranium region (P21, P22, P23)

Calvarial breadth (P21) followed a somatic, monophasic growth pattern. Overall growth in variable size increased in proportion ($b = 1$) to skull size, increasing by 49% at 10 y (RTY). Mastoid

Facing page: Figures 4-6

Figure 4a, b: Bivariate plot of log condylobasal length (mm) on: (a) log body length (cm) and (b) age (y). Solid triangles, known-age animals (MCM) based on tagging. Squares, canine aged animals (PEM).

Figure 5a, b, c: Bivariate plots of: (a) log body length (cm) on suture age; (b) log condylobasal length (mm) on suture age; (c) suture age on age (y). Solid triangles, known-age animals (MCM) based on tagging. Squares, canine aged animals (PEM).

Figure 6: Example of neural growth. Log breadth of brain case (mm) on age (y). Solid triangles, known-age animals (MCM) based on tagging. Squares, canine aged animals (PEM).

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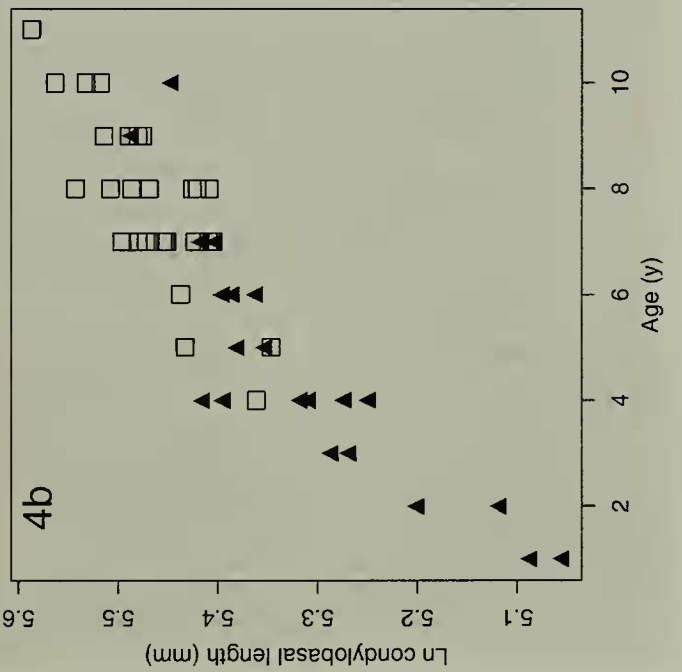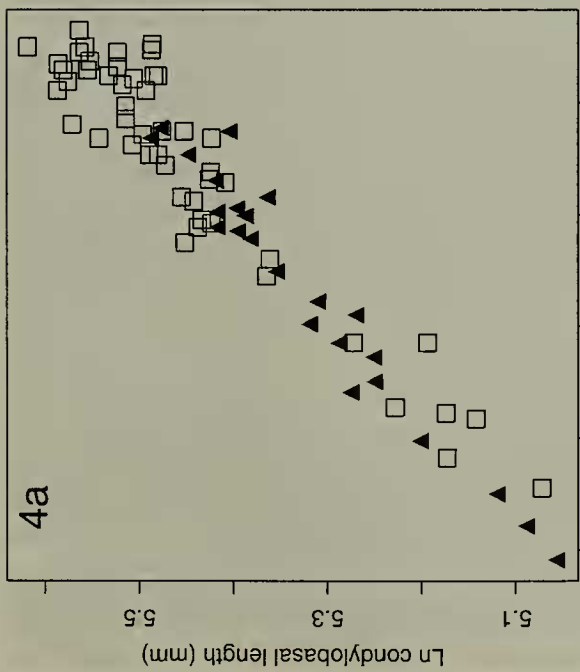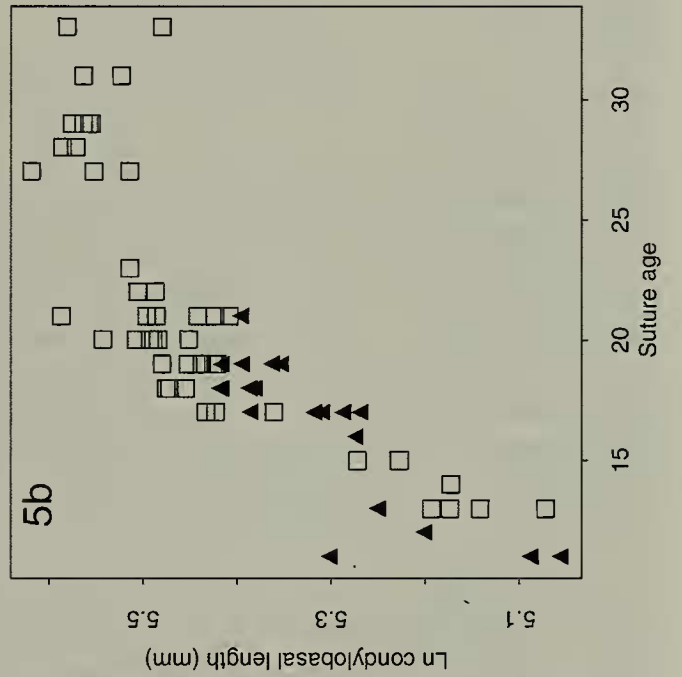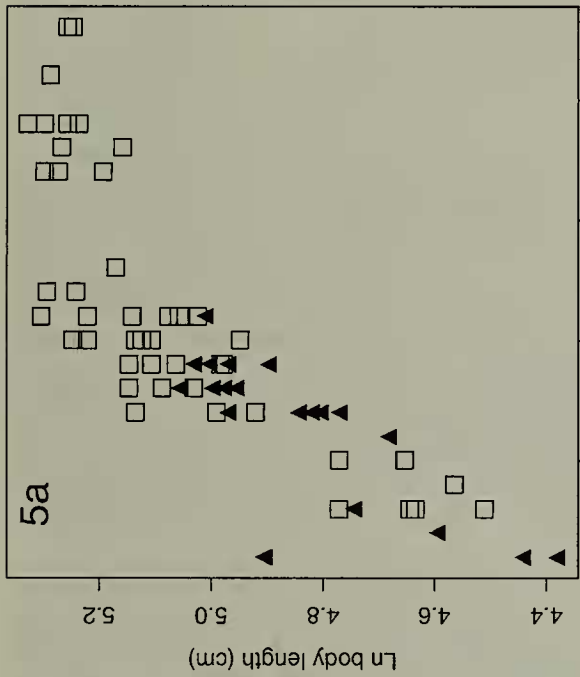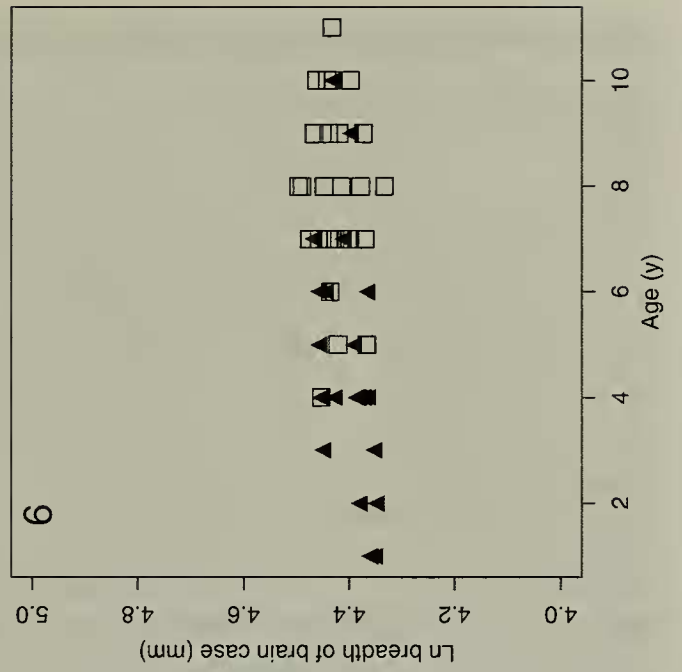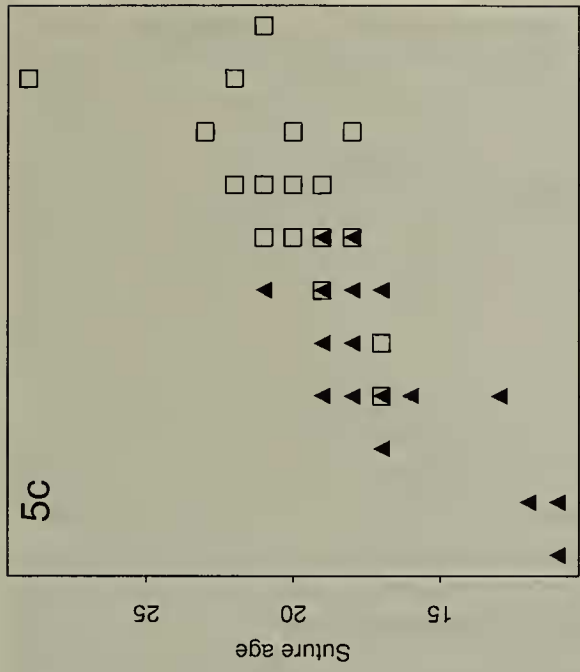
Table 5: Discriminant analysis for seal age group (sub-adult, adult) inferred from skull length

Known Age Group	Classification into age group n	Subadult (y_1) (1 y 7 months to 7 y 6 months)	Adult (y_2) ($\geq$ 7 y 7 months)
1	32	26 (81%)	3
2	29	6	26 (90%)
Total	61	32	29

Table 6: Suture index for male Cape Fur Seals according to age (y) and age group

No	Suture	Yearling				Subadults					Adults	
		10 mo	2 y	3 y	4 y	5 y	6 y	7 y	8 y	9 y	10 y	$\geq$12 y
viii	Basioccipito-basisphenoid (brain case)	1	1	4	1–4	4	4	4	4	4	4	4
i	Occipito-parietal (brain case)	1	1	3	2–4	4	3–4	4	3–4	4	4	4
ii	Interparietal (brain case)	1	1	1	1–2	1–2	1–3	1–4	1–4	2–4	3	3–4
iii	Coronal (brain case)	1	1–2	2	1–3	1–2	2–3	1–3	1–3	1–3	3	3–4
x	Squamosal-jugal (face-zygomatic)	1	1	1	1	1	1	1	1–2	1	2	3–4
vi	Premaxillary-maxillary (face-maxilla)	1	1	1	1	1	1	1	1	1	1	1–3
xi	Maxillary (face-maxilla)	1	1	1	1	1	1	1	1	1	1	1–3
ix	Squamosal-parietal (brain case)	1	1	1	1	1	1	1	1	1	1	1–3
iv	Interfrontal (brain case)	1	1	1	1	1	1	1	1	1	1	1–2
viii	Basisphenoid-presphenoid (brain case)	1	1	1	1	1	1	1	1	1	1	1
v	Internasal (face-nasal)	1	1	1	1	1	1	1	1	1	1	1
	Suture index	11	11–12	17	13–19	17–19	18–21	18–21	19–22	18–23	22	27–33
	Total no. skulls = 48	2	2	2	7	3	4	8	6	3	1	10

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breadth (P22) followed a somatic growth pattern. Overall growth scaled with positive slope (b = 1.29) relative to CBL, increasing by 80% at 10 y (RTY). A prominent secondary growth spurt was apparent at 10 y (Figure 7). Basion to bend of pterygoid (P23) followed a neural growth pattern, with most growth competed by 7 y (76 mm). Overall growth in variable size was negatively allometric relative to CBL.

Frontal region (D7, D8)

Least interorbital constriction (D7) followed a somatic, monophasic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 79% at 10 y (RTY). Most growth was completed by 9 y. Greatest breadth at supraorbital processes (D8) followed a somatic growth pattern. Overall growth scaled with a very slight positive slope (b = 1.03) relative to CBL, increasing by 50% at 10 y (RTY). A weak secondary growth spurt was apparent at 7 y.

Zygomatic arch (P14, P19)

Breadth of zygomatic root at maxilla (P14) followed a somatic, monophasic growth pattern. Overall growth was isometric relative to CBL, increasing by 24% at 10 y (RTY). Zygomatic breadth (P19) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope (b = 1.12) relative to CBL, increasing by 64% at 10 y (RTY). The ratio of zygomatic breadth to CBL was 1:1.8 in yearlings and adults. Zygomatic breadth was generally the widest part of the skull; however, mastoid breadth exceeded zygomatic breadth in 10 animals (7 subadults; 3 adults).

Splanchnocranium region (D3, L24, L25)

Gnathion to posterior end of nasals (D3) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 66% at 10 y (RTY). A weak secondary growth spurt was apparent at 10 y. Gnathion to foramen infraorbital (L24) and gnathion to posterior border of preorbital process (L25) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope (b = 1.26, 1.25) relative to CBL, increasing by 62% and 70% at 10 y (RTY), respectively.

Nasal region (D4, D5)

Width of anterior nares (D4) followed a somatic, monophasic growth pattern. Overall growth was isometric relative to CBL (Figure 8), increasing by 43% at 10 y (RTY). Greatest length of nasals (D5) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 76% at 10 y (RTY). There was some

evidence of a very slight secondary growth spurt at 10 y, but this may have been an effect of sampling. The ratio of nasal breadth to length increased from 1:1.2 (yearlings) to 1:1.5 y (10 y).

Palatal region (P10, P11, P12, P13, P15, P16, P17)

Palatal notch to incisor (P10) and gnathion to posterior end of maxilla (P13), followed a somatic growth pattern. Overall growth scaled with a very weak positive slope (b = 1.07, 1.06) relative to CBL, increasing by 70% and 61% at 10 y (RTY), respectively.

Length of upper PC tooth row (P11) followed a somatic, monophasic growth pattern. Overall growth scaled with negative slope (b = 0.84) relative to CBL, increasing by 46% at 10 y (RTY). Greatest bicanine breadth (P12) followed a somatic growth pattern. Overall growth expressed positive allometry relative to CBL, increasing by 51% at 10 y (RTY). There was some evidence of a very slight secondary growth spurt at 10 y, but this may have been an effect of sampling biases.

Breadth of palate at PC 1 (P15), 3 (P16) and 5 (P17) followed a somatic growth pattern, increasing by 89%, 47% and 72% at 10 y (RTY), respectively. Overall growth expressed strong positive allometry for breadth at PC1; positive allometry for PC5; and isometry for breadth at PC3, relative to CBL. There was some evidence of a very slight secondary growth spurt in breadth at PC5 at 10 y, but this may have been an effect of sampling. The ratio of palatal breadth at PC5 (P17) to palatal length (P10) was 1:3 in both yearlings and adults (10 y).

Mandible (M28, M29, M30, M31, M32)

Length of mandible (M28) followed a somatic, monophasic growth pattern. Overall growth scaled with positive slope (b = 1.22) relative to CBL, increasing by 79% at 10 y (RTY). Length of mandibular tooth row (M29) and length of lower post-canine row (M30) followed a neural growth pattern, with most growth completed by 7 y (table 3; 68 ± 0.6 (SE, n = 12) mm; 45 ± 0.4 (SE, n = 12) mm). Growth was negatively allometric relative to CBL (Figure 9). The ratio of the length of the lower PC row (M30) to upper PC row (P11) was 1:1.1 (yearlings) and 1:1.3 (10 y). Height of mandible at meatus (M31), and angularis to coronoideus (M32), followed a somatic growth pattern, with a weak secondary growth spurt at 10 y. Overall growth expressed strong positive allometry relative to CBL (Figure 10), with variables increasing by 130% and 105% at 10 y (RTY), respectively. Growth in vertical height of the mandible was considerably greater than that of length.

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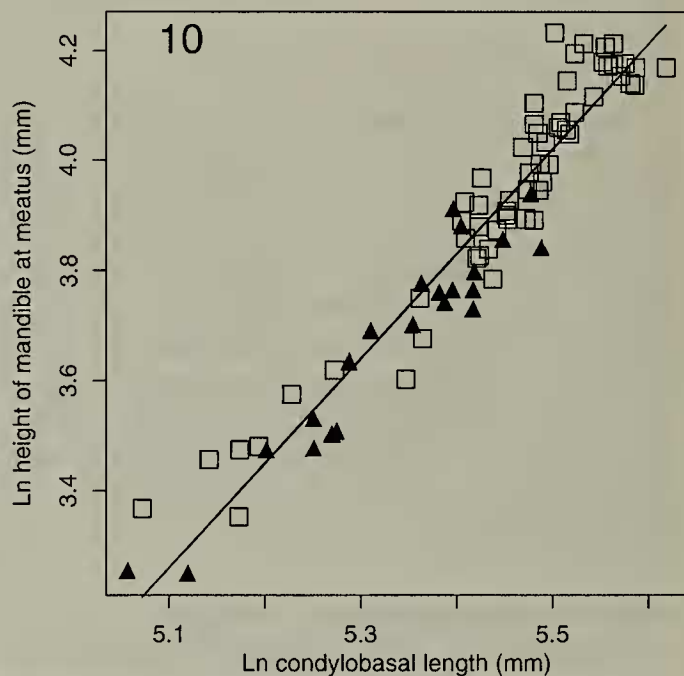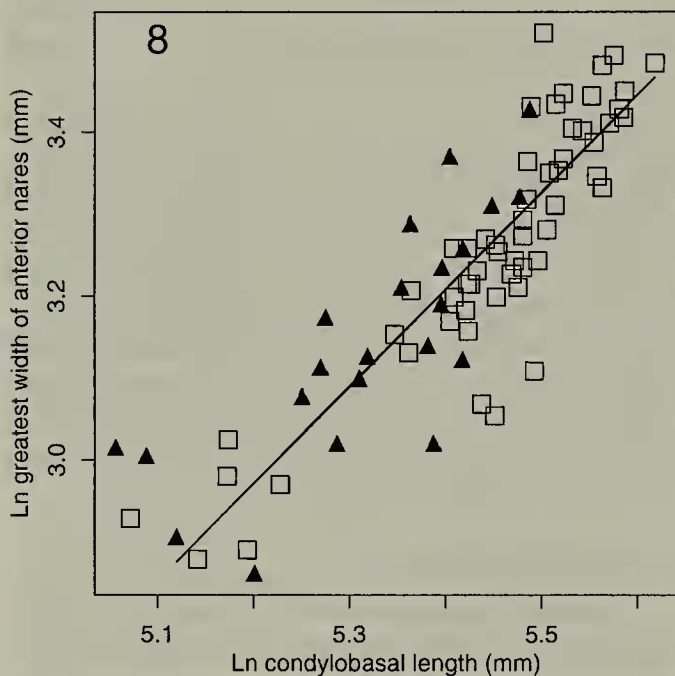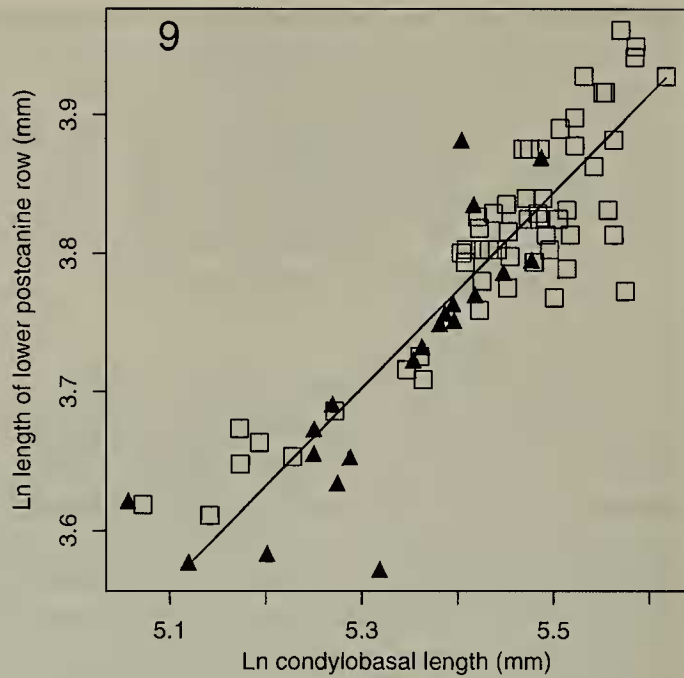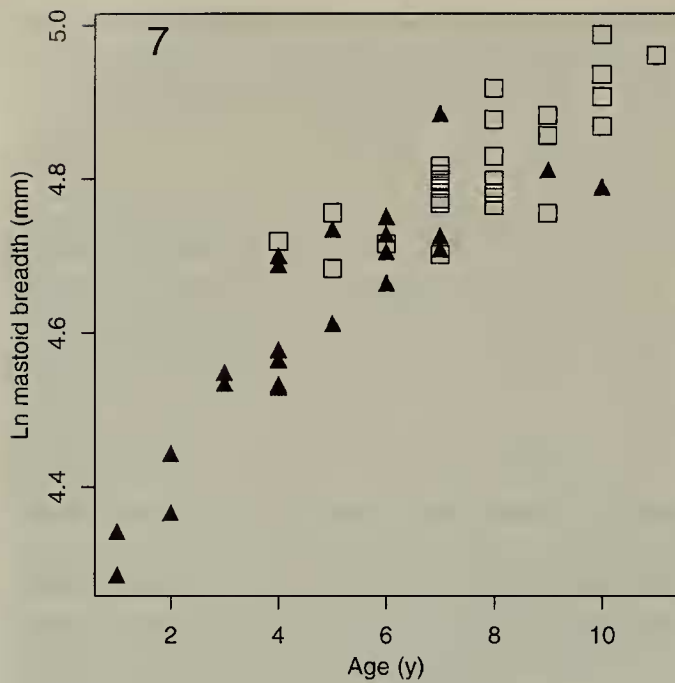
Figure 7: Example of somatic, biphasic growth. Log mastoid breadth (mm) on age (y). Solid triangles, known-age animals (MCM) based on tagging. Squares, canine aged animals (PEM).

Figure 8: Example of isometric growth. Log greatest width of anterior nares on log condylobasal length (mm). Solid triangles, known-age animals (MCM) based on tagging. Squares, canine aged animals (PEM).

Figure 9: Example of negative allometry. Log length of lower postcanine row (mm) on log condylobasal length (mm). Solid triangles, known-age animals (MCM) based on tagging. Squares, canine aged animals (PEM).

Figure 10: Example of strong positive allometry. Log height of mandible at meatus (mm) on log condylobasal length (mm). Solid triangles, known-age animals (MCM) based on tagged animals. Squares, canine aged animals (PEM).

Abnormalities

Of the 60 PEM skulls examined, 14 (23%) had a cleft palate varying in severity from slight clefts to moderate deformity (PEM: 951, 958, 1453, 1560, 1882, 2050, 2051, 2052, 2053, 2132, 2137, 2141, 2197, 2253), and abnormal bony deposits were observed on the occipital bone, at the base of the parietal in PEM2049. In addition, it was clear that the deciduous canines persist in some animals until their tenth month (i.e., AP4999). Hence the generalisations of Rand (1950) that (i) deciduous canines of pups are lost by the end of March (about 3 to 4 months old); (ii) permanent canines do not erupt from the gums before 4 months of age and are well developed by 8 months old (end of July) are not universal.

Comparison of South African and Australian Fur Seal Skulls

Comparisons were made between data on male South African fur seal skulls from the present study with published information on male Australian fur seals. King (1969) published data on condylobasal length (CBL), zygomatic width and supraorbital width (postorbital width) of male Australian fur seal skulls judged to be adult male based on their suture indices. Figures 11 and 12 are plots of King's data compared to data on South African material with a Condylobasal length greater than 180 mm. Linear egression analysis showed that both Zygomatic Width vs. CBL and Supraorbital width vs. CBL are linearly related and the Australian and South African material fall on the same regression lines:

> Zygomatic Width vs. CBL (n = 78, South African n = 36, Australian n = 42)
> Slope 0.678 ± 0.037 (Standard Error, SE)
> Intercept = -25.8 ± 9.99 mm (SE) (marginally different to zero based on t-test)
> ZYG = 0.678 x CBL - 25.8, r = 0.9252, p < 0.001
> Supraorbital Width vs. CBL (n = 73, South African n = 32, Australian n = 41)
> Slope 0.212 ± 0.026 (SE)
> Intercept = 3.98 ± 7.09 mm (SE) (not significantly different to zero)
> SOB = 0.212 x CBL + 3.98, r = 0.6898, p < 0.001

However, although the regression analyses show that the South African and Australian skulls share the same geometry it is obvious that the South African skulls are significantly smaller than the Australian material from King (1969) although there is considerable overlap: South African; CBL = 248 ± 10.7 mm (SD, n = 36), Zygomatic width = 141 ± 10.1 mm (SD, n = 36), Supraorbital width = 57 ± 5.4 mm (SD, n = 32);

Australian; CBL = 283 ± 10.7 (SD, n = 42, Zygomatic width = 166 ± 10.3 (SD, n = 42), Supraorbital width = 64 ± 5.8 (SD, n = 41). These values agree well with those published by Brunner (1998ab, Brunner 2000).

Table 7 compares the mean values for a wide range of skull parameters of South African and Australian fur seals. The Australian fur seal measurements are consistently larger than the South African skulls. However, there is one significant exception. In the present study, adult South African fur seals were found to have a braincase width (D9) of about 84 ± 2 mm (SD, n = 46) (see Table 3); this does agree with values published for South African fur seals by Brunner (1998b) (84 ± 4.6 mm, SD, n = 17) but not with the value found in her thesis (Brunner 2001) (77 ± 2, SD, n = 38). Brunner (1998b) reports the brain case width of Australian fur seals to be 78 ± 2.25 (SD, n = 45). If the braincase data of the present study shown in Table 3 was correct, then braincase size was larger in South African fur seals than that of the Australian variety. This seems exceptional and is not consistent with the differences found in the other skull parameters (Table 7). Furthermore, if the braincase was smaller in Australian fur seals, this would affect the zygomatic width measurements (Figure 1, P19) and hence the geometry of the skull. In the present study, braincase width (D9) was measured across the same section of the skull as the zygomatic width (P19) (see Figure 1). However, the graph shown in Figure 11 shows that South African and Australian fur seals have similar skull geometry. We conclude that the braincase width has been measured in a different way in the present study compared to the method used by Brunner (2001). The braincase width measure shown on the skull diagrams in the present study (D9 in Figure 1) and parameter 9 in Figure 2 in Brunner (1998a) appear to be the same but cannot have been measured in the same way. If we take the braincase width data from Brunner (2001) for both the South African and Australian fur seals we find there is no significant difference in braincase width in the two populations (Table 7).

DISCUSSION

Skull size

Arctocephalus pusillus is the largest of the fur seals, therefore the skull is correspondingly large. In the present study of the South African fur seal (*A. pusillus pusillus*), the maximum CBL was 275.4 mm (PEM898); however, skulls up to 307 mm have been reported in the Australian fur seal (*A.*
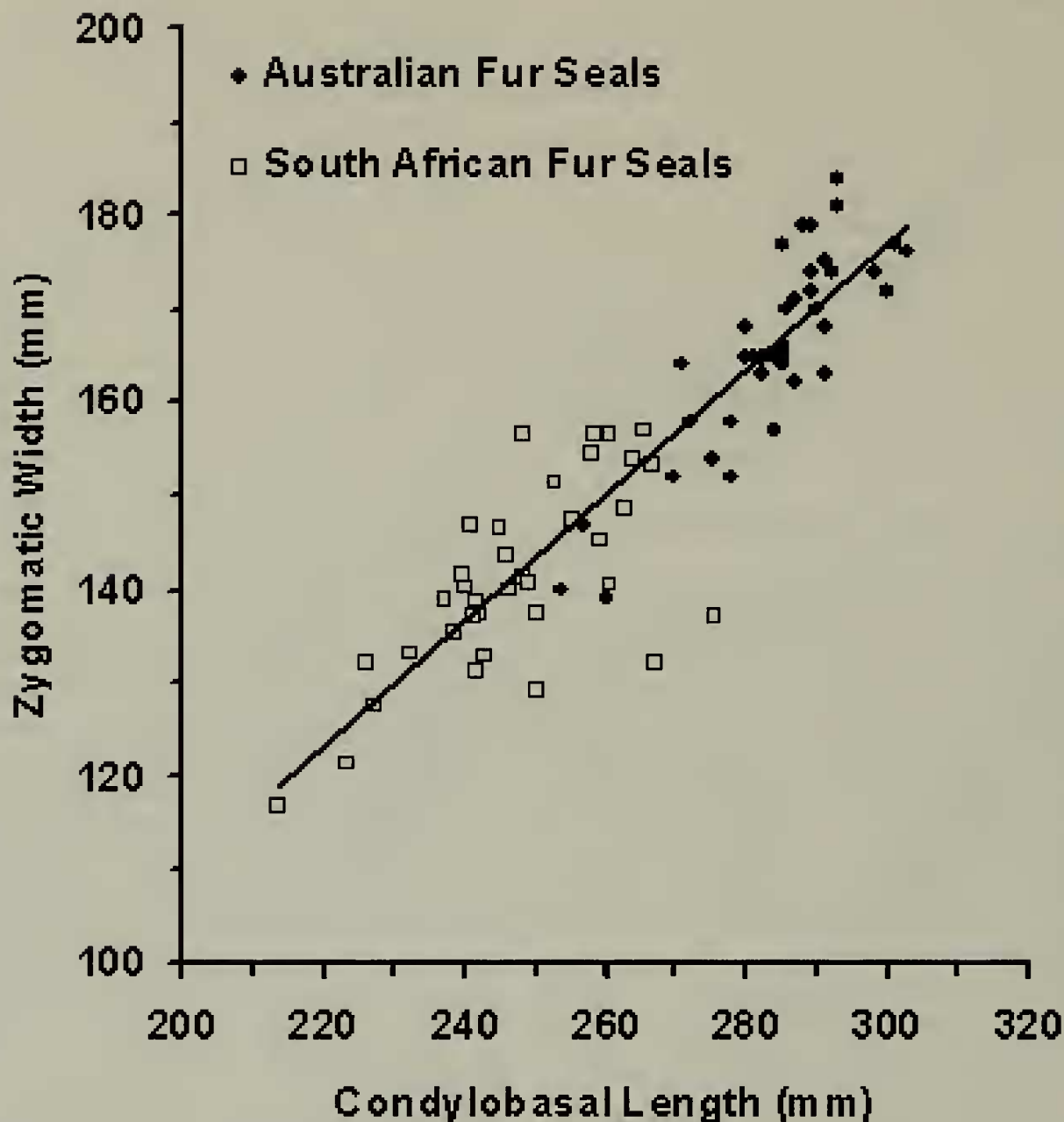
Figure 11: Comparisons of the skulls of male South African and Australian fur seals: Zygomatic arch width vs. Condylobasal length (CBL). When fitting two linear regression models to the Australian and South African fur seal data it was found that the intercepts and the slopes were not significantly different using a F-test (p = 0.08) (Draper and Smith, 1981). A single straight line could be fitted to all of the data (r = 0.9252, n = 78, p < 0.0001).

pusillus doriferus: Cruwys and Friday, 1995). As with all southern hemisphere fur seals, the skull is considerably larger in males than in females, reflecting pronounced sexual dimorphism (Bryden, 1972; King, 1972, 1983; Cruwys and Friday, 1995; Arnould and Warneke, 2002; Brunner et al., 2004). Table 7 and Figures 11 and 12 clearly indicate that male South African fur seal skulls are on average smaller than Australian fur seal skulls but Figures 11 and 12 show that they share the same geometry.

South African Fur Seals from the East Coast and West Coasts of South Africa

It has been suggested that marine mammal species inhabiting warmer waters may be smaller in body size than marine mammal species inhabiting cooler waters (Ross and Cockcroft, 1990) reflecting generally higher productivity and hence food supply in cooler waters. Long-term climatic data in Algoa Bay (South Africa), based on daily measurements, indicate that the mean water temperature is 16–17° C in winter and 21–22° C in summer. For Luderitz
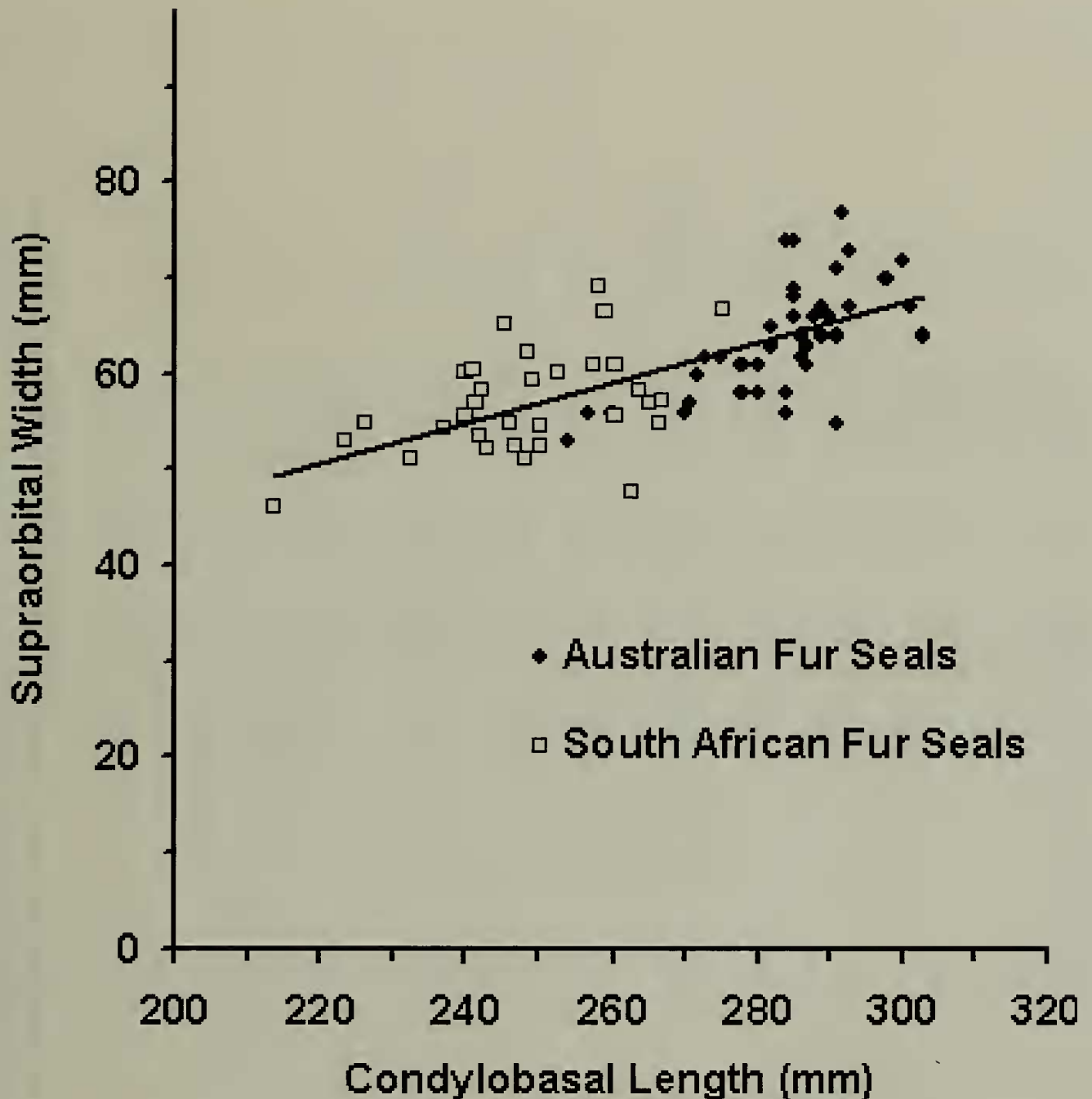
Figure 12: Comparisons of the skulls of male South African and Australian fur seals: Supraorbital width vs. Condylobasal length (CBL). Fitting two linear regression models to the Australian and South African fur seal data showed that the intercepts and the slopes were not significantly different based upon a F-test (p = 0.35) (Cochran, 1977). A single straight line could be fitted to all of the data (r = 0.6848, n = 73, p < 0.0001).

(near Sinclair Island, South Africa), mean water temperature is 12–13° C in winter and 14–15° C in summer, considerably cooler than Eastern Cape waters (Dr M. Grundlingh, pers. comm.). When comparing CBL from adult South African fur seals from these two geographic locations, we did not find sufficient reason to reject the hypothesis that the population means for skull length were equal using PEM animals ≥ 12 y. However, it is not clear if this result was influenced by a larger number of older adults in

the PEM sample. When younger PEM animals were included in the adult sample (7–12[+] y), Eastern Cape seals were found to be significantly smaller than west coast seals. Further testing using a larger sample of aged animals is required.

The larger size of the Australian fur seal (*A. pusillus doriferus*) which mainly lives in Bass Strait in Australia (Arnould and Warneke, 2002), is an argument against a straightforward relationship between body size and water temperatures (Warneke and

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Length Measurements of skull	Difference (t)	df	p-value	Mean	SD	Range	n	Code
Condylobasal length	13.50	44	<0.0005	281.7 / *245.8*	7.99 / *13.00*	265.8-302.2 / *213.7-266.8*	45 / *30*	D1
Gnathion-mid-occipital crest	9.32	37	<0.0005	248.6 / *217.2*	8.98 / *16.34*	227.5-270.5 / *184.3-241.2*	45 / *28*	D2
Gnathion – posterior end of nasals	6.36	45	<0.0005	98.66 / *88.81*	5.06 / *7.28*	86.83-107.96 / *72.1-101.8*	45 / *29*	D3
Length of nasals	5.03	53	<0.0005	50.07 / *44.23*	4.56 / *4.98*	38.40-58.30 / *34.6-54.0*	45 / *28*	D5
Gnathion – foramen infraorbitale	14.95	61	<0.0005	91.66 / *74.96*	4.77 / *4.639*	78.56-100.1 / *67.5-84.3*	45 / *29*	L24
Gnathion – caudal border of preorbital process	10.91	45	<0.0005	94.87 / *82.33*	3.87 / *5.261*	84.33-104.1 / *73.6-93.0*	45 / *28*	L25
Palatal notch – incisors	7.67	71	<0.0005	121.33 / *105.2*	11.14 / *6.94*	85.51-140.3 / *92.9-120.8*	45 / *29*	P10
Gnathion – posterior maxilla (palatal)	12.76	45	<0.0005	135.2 / *116.3*	5.03 / *6.77*	125.8-150.0 / *99.5-129.1*	45 / *28*	P13
Gnathion – caudal border postglenoid process	13.44	42	<0.0005	217.35 / *187.7*	7.16 / *10.01*	199.1-235.4 / *164.9-202.2*	45 / *27*	P18
Basion – zygomatic root	11.83	47	<0.0005	191.5 / *169.00*	6.76 / *8.51*	180.4-207.6 / *151.2-181.9*	45 / *28*	P20
Basion – bend of pterygoid	8.61	56	<0.0005	86.41 / *78.78*	3.72 / *3.593*	79.65-97.05 / *71.3-87.4*	45 / *27*	P23

Table 7: Comparison of Male Adult Australian Fur Seals (std font) with Male Adult South African Fur Seals (in italics). All comparisons Australian – South African.

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*South African fur seal summary measurements taken from Brunner (2001).

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Breadth Measurements of Skull	Difference (t)	df	p-value	Mean	SD	Range	n	Code
Breadth of nares	14.38	49	<0.0005	37.24 *28.68*	2.13 *2.711*	32.75-43.60 *24.1-33.8*	45 *29*	D4
Breadth at preorbital processes	9.32	45	<0.0005	79.29 *68.20*	4.19 *5.26*	69.44-87.71 *55.8-77.0*	45 *27*	D6
Interorbital constriction	6.51	53	<0.0005	42.71 *37.80*	3.04 *3.129*	35.59-47.80 *30.8-42.8*	45 *26*	D7
Breadth at supraorbital processes	6.86	52	<0.0005	66.17 *56.84*	5.50 *5.53*	55.66-76.07 *46.1-69.1*	45 *26*	D8
Breadth at braincase*	1.64	80	0.104	78.17 *77.40*	2.25 *2.02*	72.60-83.87 *73.20-81.07*	45 *38*	D9
Occipital crest – mastoid	18.99	35	<0.0005	150.9 *108.49*	5.39 *11.02*	117.0-140.1 *85.3-125.2*	45 *28*	L26
Height of sagittal crest	7.02	33	<0.0005	10.71 *4.722*	2.41 *3.788*	6.88-16.48 *0.0-12.0*	45 *24*	L27
Rostral width	10.73	47	<0.0005	62.18 *50.86*	3.60 *4.897*	52.37-69.76 *41.9-61.1*	45 *29*	P12
Breadth of zygomatic root of maxilla	6.92	56	<0.0005	19.01 *15.83*	1.84 *1.986*	13.56-22.46 *12.2-19.4*	45 *29*	P14
Breadth of palate at postcanines 3-4	13.56	53	<0.0005	38.53 *27.77*	3.26 *3.176*	28.90-44.49 *20.4-32.7*	44 *26*	P16
Breadth of palate at postcanine 5	7.98	51	<0.0005	39.77 *33.96*	2.78 *3.168*	35.51-45.10 *27.3-39.4*	45 *28*	P17
Zygomatic breadth	11.25	42	<0.0005	164.7 *142.4*	5.99 *9.56*	153.7-179.0 *121.4-158.9*	45 *29*	P19
Auditory breadth	10.52	62	<0.0005	135.0 *116.4*	8.53 *6.51*	120.2-179.0 *104.6-126.1*	45 *28*	P21
Mastoid breadth	12.19	36	<0.0005	158.04 *132.5*	5.72 *9.93*	147.7-170.4 *116.2-147.9*	45 *27*	P22

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Table 7 continued

Mandible and Teeth	Difference (t)	df	p-value	Mean	SD	Range	n	Code
Length of mandibular tooth row	6.89	41	<0.0005	75.15 / 68.70	3.20 / 3.876	69.23-84.17 / 59.8-75.7	41 / 24	M29
Length of lower postcanine row	7.32	56	<0.0005	51.61 / 46.77	2.56 / 2.836	43.86-57.53 / 40.8-52.5	41 / 29	M30
Height of mandible at meatus	6.58	48	<0.0005	69.03 / 58.35	5.30 / 7.65	47.66-78.04 / 39.5-68.8	41 / 30	M31
Angularis - coronoideus	7.69	46	<0.0005	68.77 / 58.07	4.35 / 6.65	56.33-76.81 / 42.3-67.1	41 / 29	M32
Length of mandible	10.26	43	<0.0005	198.1 / 173.3	7.22 / 11.50	181.7-214.6 / 141.6-192.0	41 / 29	M36

Shaughnessy, 1985; Brunner 1998ab; Brunner et al., 2002) because Bass Strait waters are considerably warmer than the South African waters where the South African variety occurs (Stewardson 2001). Arnould and Warner (2002) also point out that Bass Strait waters are also far less productive than the waters inhabited by the South African fur seal. Other closely related fur seals found in Australian, New Zealand, Subantarctic and Antarctic waters (*A. australis forsteri, A. tropicalis, A. gazella* and *A. australis*) are all smaller than *A. pusillus* (Kerley and Robinson, 1987; Brunner 1998ab; Brunner et al., 2002; Daneri et al., 2005; McKenzie et al., 2007).

Skull shape

Morphological observations of the skull were generally consistent with earlier studies by Rand (1949*b*, 1950, 1956) and Repenning et al. (1971). As for all otariids, the frontal bones project anteriorly between the nasal bones; supraorbital processes are present; the tympanic bulla are small and flat, comprised primarily of the ectotympanic; the alisphenoid canal is present; the mastoid processes are massive; the jugal-squamosal joint of the zygomatic arch overlap; and deep transverse grooves occur on the occlusal surface of the upper incisors (Burns and Fay, 1970; King, 1983; present study).

Within the species, the forehead is convex at the supraorbital region; the snout is long; the nasals are long and flared anteriorly; the palate is moderately broad and arched; the maxillary shelf at the root of the zygomatic process is very short in an anterio-posterior direction; the tooth rows are parallel, with robust, tricuspid PC, and a slight diastema between upper PC 5 and 6 (Repenning et al., 1971; present study).

As with other species of this genus, the interorbital region (D7) was less than 20% of CBL in adults (i.e., 15%); palatal notch to the incisors (P10) was more than 37% of CBL (i.e., 43%); and nasal length (D5) fell within 14% (smallest fur seal, *A. galapagoensis)* and 18% (largest fur seal, *A. pusillus pusillus* and *A. pusillus doriferus*) of CBL (i.e., 18%) (Scheffer, 1958; Cruwys and Friday, 1995; present study).

Growth Curves

Mammals typically exhibit a determinant growth pattern – as juveniles and subadults they grow in size at a fast rate when very young then growth gradually slows until it finally more or less stops as adults. Such growth patterns can usually be described by various variations of exponential or logistic growth curves of the form: exponential saturation or von Bertalanffy curve, $y = y_{max} * (1 - e^{-kt})$ or logistic growth curve, y

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$= y_{max}/(1-be^{-kt})$. Both these curves can be difficult to fit to experimental data and obtain useful estimates of y_{max} and k. Fitting usually requires values for accurately aged fully grown animals over a range of adult ages otherwise the asymptotic y_{max} may not be estimated reliably. More complex models with another unknown, for example to allow for length as infants, are even more difficult to fit.

The present study has shown that South African male fur seals continue to grow to about 10 y, only just short of the age of the oldest definitively aged individuals (tagged animals) and also just short of the maximum age that can be determined from dentition (12 y). Arnould and Warneke (2002) working on Australian fur seals had enough fully grown and aged seals to be able to fit asymptotic growth curves to their data for both males and females. Similarly, Winship et al. (2001) working on the Steller sea lion (*Eumetopias jubatus*) had access to data on hundreds of individuals aged on the basis of dentition and were able to fit SBL vs. age to both types of asymptotic growth curve.

In the present study SBL and skull parameters such as CBL when plotted against age did not show obvious asymptotes (Table 4, Figure 4b) and little curvature so maximum SBL and CBL could not be accurately determined from such curves. There were not many aged adult animals and the oldest known age was 13 years so the range of ages of fully-grown adults was small. When we did fit these exponential saturating curves to the data the residuals versus fitted values plot were not random scatters about zero indicating that the curves were not adequate models for the data. The data was better described by simple linear or Log/Log relationships.

Condylobasal length as an indicator of SBL and age

In male South African fur seals, CBL continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). The absence of very old skulls of known-age (18–20 y), made it difficult to determine overall growth in CBL. In contrast CBL continues to increase until at least 13 y in male *C. ursinus* (Scheffer and Wilke, 1953, but see Scheffer and Kraus, 1964) and slows at 10 y in male *Eumetopias jubatus* (Fiscus, 1961).

Condylobasal length was found to be a reasonable indicator of SBL and age group, but not of absolute age. The classification criteria for SBL developed in this study will be particularly useful when a seal is decomposed/scavenged (total SBL can not be measured), and/or the skull is incomplete/absent (total SBL can not be extrapolated from skull length). The classification criteria for age group will be particularly useful when teeth are not available for age determination; or museum records have been misplaced or destroyed. As more specimens become available, particularly very old tagged individuals of known age, the classification criteria could be made more precise.

Suture index as an indicator of age

Although cranial sutures close progressively with age, suture age was not considered to be a good indicator of chronological age (y) or age group (sub-adult/adult). Similar observations have been made in other male otariids, e.g., in *C. ursinus,* the rate of suture closure is highly variable, and like SBL and CBL, is a poor indicator of chronological age (Scheffer and Wilke, 1953) compared to teeth (Scheffer, 1950; McCann, 1993; Oosthuizen, 1997). Brunner et al. (2004) in their study of suture closure sequences in several fur seal species was also hesitant to use suture closure indices to indicate chronological age although they were perhaps more confident in using it to assign skulls to age groups than is warranted from the conclusions drawn from the present study. A particular problem is that canine-tooth sections are only useful for aging individuals up to 12 years old and yet some individuals at that age still have some incomplete closure of sutures. Some individuals probably live considerably longer than 12 years but skulls from very old animals are not currently available.

Function and growth
Neurocranium region

In mammals, growth of the protective brain case corresponds closely to that of the enclosed brain (Moore, 1981). The brain/brain case grows rapidly during prenatal and postnatal life; attains full size early in development before that of the basicranium or face; and scales with negative slope relative to skull size (Moore, 1966, 1981; Bryden, 1972; King, 1972; Gould, 1975; Moore and Lavelle, 1975; Enlow, 1982; Shea, 1985; Wayne, 1986; Hartwig, 1993; Morey, 1990; present study). Early maturation of the brain/brain case is essential for nervous control of the body.

The sagittal crest strengthens the skull, and provides an increased surface area for muscle attachment. In adults, large crest size is advantageous in combat behaviour between breeding bulls, and in feeding (increases bite force). Sagittal crest height begins to increase in size at 4–7 y (highly variable), reaching at least 12 mm in some adult males. In male *Zalophus californianus,* the sagittal crest begins to

develop at 5 y, with height ranging from 11–36.5 mm in adults (Orr et al., 1970). In male *Eumetopias jubatus*, sagittal crest height ranged from 7–37 mm in adults (Fiscus, 1961). The wide variance in crest height in older South African fur seal males is possibly an artefact of the unknown actual age of bulls classed as >12y based on dentition. It is also possible that it might reflect differences between breeding and non-breeding bulls in the collection of skulls used in the present study.

Basicranium region

The basicranium accommodates the hearing apparatus (Enlow, 1982). As with other mammals, growth of the otic capsule (and associated structures) appears to follow a neural growth pattern (Bast and Anson, 1949; Hoyte, 1961; Moore, 1981). Early development of the otic capsule enables juveniles to recognise the 'pup-attraction call' of their mothers. Mother-pup recognition is critical for pinnipeds living within a colony where separation is frequent, and mother-pup pairs are numerous (see Rand, 1967; Trillminch, 1981; Oftedal et al., 1987; Bowen, 1991).

Unlike the otic capsule, calvarial breadth and mastoid breadth mature much later in life (present study). In adults, enlarged mastoids are advantageous in combat behaviour between breeding bulls, and in feeding (large head size/increases bite force); and facilitate directional hearing (provides a greater surface area of specific orientation for selective reflection of sound) (Repenning, 1972).

Frontal region

The interorbital region provides the structural base for the snout (Enlow, 1982). The dimensions of this region increase with age to accommodate the development of the proportionally large snout.

The supraorbital processes strengthen the skull (very thick in adults), protects the orbital region, and increases bite force. In adult seals, this enlarged structure is advantageous in feeding, and in combat behaviour between breeding bulls.

Zygomatic arch

The zygomatic arch protects the eye, provides a base for the masseter and part of the temporal muscle, accommodates conductive hearing (squamous root) and is the point of articulation for the mandible (Evans, 1993; Repenning, 1972). As with other mammals, the zygomatic arch enlarges laterally and inferiorly to accommodate enlargement of the head, and a correspondingly greater temporal muscle mass (Moore, 1981; present study).

The orbital border of the zygomatic bone forms the ventral margin of the eye socket. As with other pinnipeds, the orbits were large to accommodate large eyes (King, 1972). In South African fur seals, the horizontal diameter of the eye is *c.* 40 mm (e.g., animals AP5215, 2 y 4 months; AP5210, 3 y). Although large eyes are potentially advantageous in the detection of benthic and/or fast moving pelagic prey (David, 1987), vision is not necessary to locate/capture prey in seals (see King, 1983).

Splanchnocranium region

In South African fur seals, lateral face length and width of snout at the canines, scaled with positive slope relative to CBL, similar to that of wild canids (Lumer, 1940; Wayne 1986; Morey, 1990; Evans, 1993). As the face and snout increased in length, the brain case and orbits became proportionally smaller.

In mammals, the size and shape of the brain establishes boundaries that determine the amount of facial growth; and special sense organs housed within the face influence the direction of growth (Enlow, 1982). In adult South African fur seals, the brain is relatively large and more spherical than in terrestrial carnivores (Lumer, 1938; Harrison and Kooyman, 1968; King, 1983; Evans 1993), yet long and narrow compared to humans and other primates (i.e., small cerebrum) (Scott 1951; Gould 1975; Moore and Lavelle 1975; Shea 1985; Sirianni and Swindler, 1985). Therefore, the snout is correspondingly long and narrow. The wide nasal openings were aligned in a horizontal plane with the nerves of the olfactory bulb; and the orbital axis is pointed straight forward in the direction of body movement (Enlow, 1982; present study).

Nasal and palatal region

The naso-maxillary complex is the facial part of the respiratory (nasal cavity) and alimentary (oral cavity) tracts, which also facilitates sound production and the sense of smell. The floor of the nasal cavity forms the roof of the oral cavity, thus growth of the two cavities was highly coordinated. Growth was predominantly somatic, with similar allometric trends to those of wild canids (Lumer, 1940; Wayne, 1986; Morey, 1990). Progressive growth of this region is needed to accommodate the large dental battery.

Growth of dentition has been described by Rand (1950, 1956). At 6 to 12 months, South African fur seals gradually transfer from milk to solids (fish, crustacean and cephalopod) (Warneke and Shaughnessy, 1985). Although the small, deciduous teeth are usually lost by the end of the first 5 months (Rand, 1956), deciduous canines may persist for 10 months (present study). The permanent teeth are used

to hold slippery prey (gripping), and to reduce prey size (biting and shearing) and of course in fighting between rival males. Growth of the permanent teeth is a gradual process, with diet becoming more varied with age and experience (Rand, 1959). In the upper jaw, the canines protrude beyond the tip of the 3rd upper incisor only in the 2nd y (Rand, 1956).

In male South African fur seals, the ability to produce sound is evident at birth, with vocal skills broadening with increased age (Rand, 1967). In otariids, the production of sound is important in mother-pup recognition; communicating within a colony; and affirmation of territorial boundaries and social status (e.g., Stirling and Warneke, 1971).

Although the olfactory area is reduced when compared to terrestrial carnivores, the sense of smell appears to be well developed, and plays an important role in the detection of sexually receptive females, and land predators (Harrison and Kooyman, 1968; Peterson, 1968; King, 1983; Renouf, 1991; Wartzok, 1991).

Mandible

Using human anatomy as a model, the horizontal part of the mandible (corpus) provides the structural basis for tooth formation, and the vertical part (ramus = condyle, angular process, coronoid process, masseteric fossa) provides areas for articulation and muscle attachment (Scott, 1951).

As with other carnivores, the ramus increased substantially in height to accommodate implantation of the teeth, and expansion of the nasal region (Evans, 1993; Enlow, 1982; present study). The coronoid process grew upwards and backwards increasing in thickness on the anterior borders; the condyles grew backwards, beyond the level of the coronoid process; and the masseteric fossa formed a large, deep depression for jaw muscle (masseter and temporalis) attachment. Large jaws and jaw muscles are advantageous in feeding and in combat behaviour between breeding bulls (increases bite force/increases gape).

In mammals, the mandible of newborns is proportionally smaller than the upper jaw, and therefore must grow at a slightly faster rate to provide anatomical balance (Scott, 1951; Enlow, 1982). In order to achieve correct occlusal relationships between upper and lower dentition, the rate of growth between the mandible and maxilla needs to be highly coordinated (Scott, 1951; Bryden, 1972; Moore, 1981; Enlow, 1982; Hartwig, 1993; Brunner et al., 2004). In South African fur seals, the PC teeth are robust, therefore the tooth row is long compared to other fur seals and other carnivores such as dogs (Rand, 1950;

Scott, 1951; Scheffer and Kraus, 1964; Bryden, 1972; Burns and Fay, 1970; Enlow, 1982; Wayne, 1986; Hartwig, 1993; McCann, 1993; Cruwys and Friday, 1995; Oosthuizen, 1997; Brunner, 1998ab; Brunner et al., 2002; Brunner et al., 2004; Daneri et al., 2005).

Growth rate of the lower PC row ($b = 0.7$) was similar to that of the upper PC row ($b = 0.8$), relative to CBL. Overall percent increase in growth was greater in the upper jaw because there are 6 PC in the upper jaw and only 5 in the lower jaw. The ratio of length of the lower PC row to upper PC row was 1:1.1 in yearlings, and increased to 1:1.3 in adults (at 10 y). Growth of the anterior dentition was considerably greater than that of the PC, due to development of the large canines.

Information presented in this study confirms earlier descriptions of the South African fur seal skull (Rand, 1949b, 1950, 1956; Repenning et al., 1971), and provides new information on skull growth according to age (y), not available for most seal species. In male South African fur seals, CBL continued to increase until at least 12 y, with no obvious growth spurt at social maturity (8–10 y). Growth of the skull was a differential process and not simply an enlargement of overall size. Components within each region matured at different rates and grew in different directions. Apart from the dentition, all variables of the facial skeleton followed a somatic growth trajectory, and most variables were positively allometric with CBL. Breadth of braincase and basion to bend of pterygoid followed a neural growth trajectory and scaled with negative slope relative to CBL. Condylobasal length and suture age were found to be poor indicators of absolute age. However, CBL was a reasonable indicator of SBL and age group.

Further information is needed on cranial capacity; orbital size; tooth eruption; and the development of the sagittal crest in relation to chronological age and social status. Meaningful biological, evolutionary and functional inferences on skull growth can only be made when similar quality data is available for other pinniped species of known-age in particular the Australian fur seals (*A. pusillus doriferus*) and New Zealand (*A. australis forsteri*). Multivariate statistical procedures can then be employed to summarise morphometric relationships within and among populations.

Table 7 and Figures 11 and 12 clearly indicate that the male South African fur seal skulls in the present study are smaller than available material from their Australian relatives. Some caution is necessary in drawing the conclusion that the male South African fur seal is indeed always smaller than the male Australian

fur seal. There is considerable overlap in skull sizes, particularly the ranges of the measurements (Table 7). In the present study, the South African skull material represented material collected from breeding colonies, stranded animals, animals killed by fishing boat crews and animals that had been tagged as pups. Most of the material used by King (1969), Crowys and Friday (1995), Brunner (1998ab), Brunner (2000) and Brunner et al. (2002) were museum specimens; mainly "beachmaster" breeding males shot at breeding colonies. The Australian skull material is therefore biased towards large breeding males and probably also by the so-called "trophy effect" where collectors tend to choose the largest specimens. The trophy effect is compounded in the case of seals by their social behaviour: breeding male fur seals "beachmasters" exclude smaller non-breeding "bachelor" males from colonies. Arnould and Warneke (2002) made a deliberate effort to collect a range of sizes of seals to avoid this problem.

There are also good biological reasons for supposing that Australian fur seals are better fed than their South African relatives. The modern South African fur seal population has grown to near the estimated population before commercial exploitation but the Australian fur seal is still rapidly recovering from near-extinction and so it is unlikely that individuals are limited in size by resource limitations (Arnould et al., 2003). Today mass starvation of South African fur seals occurs at irregular intervals as a knock-on effect of failures of upwelling currents (Anselmo et al., 1995). It is also possible that Australian fur seals are longer lived (see Arnould and Warneke 2002), which might again reflect a population not yet fully recovered to their original numbers. From these considerations it is reasonable to conclude that the South African material is more representative of a stable population of male South African fur seals than the corresponding male Australian fur seal material.

Historically the separation of the South African and Australian fur seals into subspecies was mainly based on them having non-overlapping geographical distributions and only minor differences such as a slight difference in size (Australian fur seals seem to grow slightly larger (& longer lived?), Cruwys and Friday, 1995; Brunner 1998ab; Arnould and Warneke, 2002; Brunner et al., 2002; Brunner 2003; Brunner et al., 2004). Recent molecular evidence supports their varietal status as two very closely related but distinct populations (Wynen et al., 2001). This implies that the Australian population is of geologically recent origin from South African immigrants.

Do stragglers from South Africa reach Australian waters today? Identification of fur seals until recently was largely based on provenance because it was difficult to separate some species based on classical taxonomy (Brunner 2003). Thus, where distributions overlap, for example the Australian (*A. pusillus doriferus*) and New Zealand fur seal (*A. australis forsteri*), there can be difficulties in positive identification, particularly of immature individuals (King 1969; Brunner 2003). Understandably, stragglers outside their normal range can be difficult to identify. Recently some molecular biological information on the interrelationships of otariid seals has become available (Wynen et al., 2001; Lancaster et al., 2006). Both the South African and Australian fur seals are thought to be less wide-ranging than their Subantarctic and Antarctic cousins (*A. tropicalis* and *A. gazella*) and largely remain in coastal waters. On the other hand, Warneke and Shaughnessy (1985) state that South African fur seals are known to forage at least 220 kilometres offshore. Molecular evidence (Wynen *et al.*, 2001) does not refute the possibility that contempory South African fur seals do occasionally reach Australia and breed with the local population. Lack of evidence of stragglers from South Africa turning up in Australian waters should not be construed as proof that this does not occur today. Given an *A. pusillus* skull of unknown provenance it would not be possible to confidently assign it to *A. pusillus pusillus* or *A. pusillus doriferus* on the basis of current morphometric or molecular taxonomy (Wynen et al., 2001; Brunner et al., 2002; Brunner 2003). The two varieties of *A. pusillus* are so similar that only finding a tagged individual from South Africa in Australia would settle the issue.

The biogeography of ocean roaming fur seals is not static. For example, Macquarie Island, after its original fur seal population (specie(s) undetermined?) was wiped out in the 19th century, has been repopulated by three species of fur seals (*A. australis forsteri, A. tropicalis* and *A. gazella*). These three species are known to be hybridising although the breeding success of the hybrids is not high (Lancaster et al., 2006). The closest sources of the Antarctic and Subantarctic fur seal colonists are several thousand kilometres away. Similarly, straggler Subantarctic fur seals (*A. tropicalis*) periodically appear on the South African coast (Shaughnessy and Ross, 1980) and in Southern Australia (King, 1983; Kirkwood et al., 1992).

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APPENDIX 1: South African fur seals (n = 83) examined in this study. Animals were collected from the coast of southern Africa between December 1982 and July 1997.

Key to sites of collection: WC (west coast), north of Cape Point Lighthouse (34o 21' S, 18o 29'E); SWC (south west coast), south of Cape Point Lighthouse to Cape Agulhas (34 o 50' S, 20 o 00' E); SC (south coast), east of Cape Agulhas, but excluding the Eastern Cape; and ECP (Eastern Cape Province), Plettenberg Bay (34 o 03' S, 23 o 24' E) to East London (33o 03' S, 27 o 54' E), Durban (29o 50' S, 31o 00' E).

Key to circumstances of collection: **Stranding** - animal washed up dead on beach (n = 38). **By-catch** - animal incidentally caught in a commercial trawl net during fishing operations (n = 37). **Sci. permit** - animal collected under scientific permit (n = 3). **Died in Rehab.** - animal died during rehabilitation at the Port Elizabeth Oceanarium (n = 3). **Other** – other causes of death (PEM958 found floating in the ocean off Humewood beach). **Not Recorded** - Circumstances not recorded.

	ID No.	Date of collection	Approximate location	Region	Circumstances of collection	SBL (cm)
1.	PEM898	22 Dec 82	1 km E of Van Starden's River Mouth, St. Francis Bay (FB)	ECP	stranding	200
2.	PEM916	Jan 1983	Willows, Port Elizabeth (PE) (34° 03'S, 25° 35'E)	ECP	stranding	91
3.	PEM917	11 Jan 83	2 km W of Maitland River Mouth, FB	ECP	stranding	104
4.	PEM951	16 May 83	35 km E of Sundays River Mouth, Woody Cape (WC)	ECP	stranding	170
5.	PEM958	13 Dec 83	Humewood, PE (33° 59'S, 25° 40'E)	ECP	other	190
6.	PEM975	7 Oct 83	40 km E of Sundays River Mouth, WC	ECP	stranding	172
7.	PEM1073	12 Sep 84	Oyster Bay (34° 10'S, 24° 39'E)	ECP	stranding	133
8.	PEM1453	30 Jan 88	3 km E Kabeljous River Mouth, Jeffreys Bay	ECP	stranding	193
9.	PEM1507	5 Feb 88	Kings Beach, PE (33° 58'S, 25° 39'E)	ECP	stranding	198
10.	PEM1560	26 Oct 88	Seaview (34° 01'E, 25° 17'S)	ECP	stranding	201
11.	PEM1587	18 May 89	Amsterdamhoek (33° 52'S, 25° 38'E)	ECP	stranding	192
12.	PEM1698	12 Apr 90	25 km E of Sundays River Mouth (WC)	ECP	stranding	190
13.	PEM1704	19 June 90	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	not recorded	147
14.	PEM1868	24 Sep 91	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	199
15.	PEM1877	2 Apr 92	Lauries Park, PE (34° 02'S, 25° 23'E)	ECP	stranding	185
16.	PEM1879	13 Apr 92	Flat Rocks, PE (34° 00'S, 25° 42'E)	ECP	stranding	200
17.	PEM1882	6 May 92	King's Beach, PE (33° 58'S, 25° 39'E)	ECP	stranding	180
18.	PEM1890	13 July 92	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	192
19.	PEM1891	18 July 92	Hobie Beach, SE of King's Beach (33° 58'S, 25° 39'E)	ECP	died in rehab.	137
20.	PEM1892	27 July 92	Sardinia Bay (34° 02'S, 25° 29'E), 800 m E of boat shed	ECP	stranding	185
21.	PEM1895	29 July 92	Cape Recife, PE (34° 02'S, 25° 42'E), 2 km E of lighthouse	ECP	stranding	188
22.	PEM2004	25 July 92	EC trawl grounds (34° 45'S, 24° 18'E-34° 48'S, 24° 00'E)	ECP	by-catch	-

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#	ID	Date	Location	Region	Cause	Value
23.	PEM2006	13 Aug 92	EC trawl grounds (34° 45'S, 24° 25'E-34° 42'S, 24° 40'E)	ECP	by-catch	-
24.	PEM2007	14 Aug 92	EC trawl grounds (34° 42'S, 24° 51'E-34° 42'S, 24° 42'E)	ECP	by-catch	-
25.	PEM2008	14 Aug 92	EC trawl grounds (34° 41'S, 24° 42'E-34° 38'S, 24° 54'E)	ECP	by-catch	-
26.	PEM2009	22 Aug 92	EC trawl grounds (34° 41'S, 24° 45'E-34° 37'S, 24° 59'E)	ECP	by-catch	-
27.	PEM2010	22 Aug 92	EC trawl grounds (34° 47'S, 24° 11'E-34° 46'S, 24° 25'E)	ECP	by-catch	-
28.	PEM2013	14 Sep 92	EC trawl grounds (34° 24'S, 25° 50'E-34° 25'S, 26° 02'E)	ECP	by-catch	-
29.	PEM2014	25 Sep 92	EC trawl grounds (34° 23'S, 26° 04'E-34° 23'S, 25° 58'E)	ECP	by-catch	-
30.	PEM2035	11 Mar 93	The Pipes, SE of Pollock Beach (33° 59'20"S, 25° 40' 30"E)	ECP	stranding	118
31.	PEM2036	19 Mar 93	Black Rocks, Algoa Bay (AB) (33° 50'S, 26° 15'E)	ECP	stranding	-
32.	PEM2044	28 May 93	Seaview (34° 01'S, 25° 17'E), Otter Pools	ECP	stranding	206
33.	PEM2045	30 May 93	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	145
34.	PEM2046	19 May 93	EC trawl grounds (35° 09'S, 21° 28'E)	ECP	by-catch	141
35.	PEM2048	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E-34° 50'S, 23° 40'E)	ECP	by-catch	157
36.	PEM2049	7 June 93	Kini Bay, Western Beach (34° 01'S, 25° 26'E)	ECP	stranding	174
37.	PEM2050	8 June 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	ECP	stranding	165
38.	PEM2051	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E'34° 45'S, 24° 20'E)	ECP	by-catch	168
39.	PEM2052	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E'34° 45'S, 24° 20'E)	ECP	by-catch	171
40.	PEM2053	28 June 93	EC trawl grounds (34° 46'S, 24° 21'E'34° 44'S, 24° 32'E)	ECP	by-catch	153
41.	PEM2054	29 June 93	EC trawl grounds (34° 45'S, 24° 28'E'34° 47'S, 24° 18'E)	ECP	by-catch	165
42.	PEM2081	19 July 93	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	162
43.	PEM2082	July 93	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	176
44.	PEM2087	17 Aug 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	ECP	stranding	190
45.	PEM2132	20 Dec 93	Woody Cape, AB (33° 46'S, 26° 19'E)	ECP	stranding	195
46.	PEM2137	5 Jan 94	Summerstrand, PE (34° 00'S, 25° 42'E)	ECP	died in rehab.	118
47.	PEM2140	17 Jan 94	40 km E of Sundays River Mouth, WC	ECP	stranding	187
48.	PEM2141	17 Jan 94	39 km E of Sundays River Mouth, WC	ECP	stranding	198
49.	PEM2143	21 Jan 94	Seaview (34° 01'S, 25° 17'E)	ECP	stranding	189
50.	PEM2151	3 Feb 94	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	194
51.	PEM2197	12 July 94	Cape Recife, PE (34° 02'S, 25° 42'E)	ECP	stranding	160
52.	PEM2198	July 94	Plettenberg Bay (34° 03'S, 23° 24'E)	ECP	stranding	105
53.	PEM2201	5 July 94	Schoenmakerskop (34° 02'S, 25° 32'E)	ECP	stranding	103
54.	PEM2238	July 1994	Durban (29° 50'S, 31° 00'E)	Durban	died in rehab.	96
55.	PEM2248	12 Aug 94	Seaview (34° 01'S, 25° 27'E)	ECP	stranding	158
56.	PEM2252	22 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	172
57.	PEM2253	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	152
58.	PEM2254	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	146
59.	PEM2257B	8 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	ECP	by-catch	170

No.	Catalogue	Date	Location	Region	Method	Measurement
60.	MCM1565	25 Sep 84	2 miles offshore the Vondeling area (33° 18'S, 18° 06'E)	WC	sci. permit	118
61.	MCM1786	30 Sep 94	St Helena Bay	WC	stranding	85
62.	MCM1809	14 Nov 84	Kleinzee	WC	sci. permit	173
63.	MCM1810	12 Feb 84	Kleinzee	WC	sci. permit	172
64.	MCM2763	10 Feb 85	Doringbaai area (31° 30'S, 16° 30'E)	WC	by-catch	127
65.	MCM2795	27 July 88	Demersal fishing grid 502	SWC	by-catch	158
66.	MCM3582	6 June 86	Offshore Dassen Island (33° 21'S, 17° 40'E)	WC	by-catch	142
67.	MCM3586	22 Apr 86	8 miles off Wilderness	SC	by-catch	144
68.	MCM3587	5 June 86	25 nm west of Mossel Bay	SC	by-catch	145
69.	MCM3636	17 July 87	West of Dassen Island (37° 45'S, 17° 35'E)	WC	by-catch	148
70.	MCM4365	13 Mar 90	3.5 nm off Gouritz River Mouth (34° 23'S, 21° 51'E)	SC	by-catch	124
71.	MCM4388	23 Oct 90	20 nm south of Gouritz River Mouth (34° 26'S, 21° 53'E)	SC	by-catch	122
72.	MCM4577	17 Jan 94	Cape Town Harbour	WC	stranding	150
73.	MCM4595	17 Oct 95	Off Cape Point (34° 45'S, 21° 49'E)	SW	by-catch	134
74.	MCM4597	15 Sep 95	South of Dassen Island (33° 30'S, 17° 40'E)	WC	by-catch	170
75.	MCM4989	14 Aug 96	St Helena	WC	by-catch	99
76.	MCM4992	13 Sep 96	Demersal fishing grid 493 (35° 30'S, 18° 56'E)	SW	by-catch	165
77.	MCM4996	28 Sep 96	Offshore Saldahna Bay (33° 10'S, 17° 14'E)	WC	by-catch	115
78.	MCM4999	10 July 96	Seal Island, St Helena Bay	WC	by-catch	80
79.	MCM5002	10 Jun 96	Offshore Saldahna Bay (33° 16'S, 17° 07'E)	WC	by-catch	108
80.	MCM5133	14 Jan 97	Offshore Plettenberg Bay (34° 30'S, 23° 30'E)	ECP	by-catch	153
81.	MCM5135	23 July 97	Offshore Stompneus Lighthouse	WC	stranding	110
82.	MCM5136	15 July 97	Offshore St Helena Bay (32° 27'S, 17° 38'E)	WC	by-catch	149
83.	MCM5145	Nov 94	St Helena Bay	WC	by-catch	90

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APPENDIX 2. 'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on log standard body length. Hypothesis testing on regression slopes: Ho:ß = 1 vs. H1:ß < 1 or H1:ß > 1. Tested at the p < 0.05 level, ns signifies not significant.

Dependent variable	Linear regression				Allometry		
	n	Intercept ± S.E.	Slope ± S.E.	r (p)	Alternative hypothesis	d.f.	p
Dorsal							
D1 Condylobasal length	74	2.65 ± 0.08	0.55 ± 0.02	0.93 (0.00)	H_1; ß < 1	72	0.00
D2 Gnathion to middle of occipital crest	73	2.51 ± 0.11	0.55 ± 0.02	0.93 (0.00)	NA	NA	NA
D3 Gnathion to posterior end of nasals	71	1.12 ± 0.12	0.65 ± 0.02	0.92 (0.00)	NA	NA	NA
D4 Greatest width of anterior nares	71	0.16 ± 0.19	0.61 ± 0.04	0.88 (0.00)	H_1; ß < 1	69	0.00
D5 Greatest length of nasals	70	0.19 ± 0.20	0.69 ± 0.04	0.85 (0.00)	H_1; ß < 1	69	0.00
D6 Breadth at preorbital processes	69	0.85 ± 0.13	0.65 ± 0.03	0.90 (0.00)	NA	NA	NA
D7 Least interorbital constriction	69	-0.04 ± 0.16	0.70 ± 0.03	0.88 (0.00)	H_1; ß < 1	67	0.00
D8 Breadth at supraorbital processes	65	1.07 ± 0.18	0.57 ± 0.04	0.86 (0.00)	H_1; ß < 1	63	0.00
D9 Breadth of brain case	71	3.95 ± 0.09	0.10 ± 0.02	0.40 (0.00)	NA	NA	NA
Palatal							
P10 Palatal notch to incisors	73	1.56 ± 0.15	0.60 ± 0.03	0.86 (0.00)	H_1; ß < 1	71	0.00
P11 Length of upper postcanine row	73	1.70 ± 0.15	0.46 ± 0.03	0.77 (0.00)	NA	NA	NA
P12 Greatest bicanine breadth	73	0.58 ± 0.16	0.64 ± 0.03	0.92 (0.00)	H_1; ß < 1	71	0.00
P13 Gnathion to posterior end of maxilla	73	1.74 ± 0.10	0.58 ± 0.02	0.91 (0.00)	H_1; ß < 1	71	0.00
P14 Breadth of zygomatic root of maxilla	74	0.45 ± 0.27	0.44 ± 0.05	0.74 (0.00)	H_1; ß < 1	72	0.00
P15 Breadth of palate at postcanine 1	72	-1.16 ± 0.25	0.84 ± 0.05	0.89 (0.00)	H_1; ß < 1	70	0.001
P16 Breadth of palate at postcanine 3	72	0.21 ± 0.19	0.60 ± 0.04	0.87 (0.00)	H_1; ß < 1	70	0.00
P17 Breadth of palate at postcanine 5	71	-0.02 ± 0.18	0.68 ± 0.04	0.87 (0.00)	H_1; ß < 1	69	0.00
P18 Gnathion to hind border of postglenoid process	72	1.88 ± 0.08	0.65 ± 0.02	0.93 (0.00)	NA	NA	NA
P19 Bizygomatic breadth	74	1.69 ± 0.12	0.62 ± 0.02	0.91 (0.00)	NA	NA	NA
P20 Basion to zygomatic root (anterior)	72	2.36 ± 0.07	0.53 ± 0.01	0.93 (0.00)	NA	NA	NA
P21 Calvarial breadth	72	1.76 ± 0.09	0.58 ± 0.02	0.94 (0.00)	NA	NA	NA
P22 Mastoid breadth	72	1.15 ± 0.11	0.72 ± 0.02	0.93 (0.00)	NA	NA	NA
P23 Basion to bend of pterygoid	72	2.52 ± 0.08	0.36 ± 0.02	0.91 (0.00)	H_1; ß < 1	70	0.00

Lateral

L24 Gnathion to foramen infraorbital	73	0.85 ± 0.14	0.67 ± 0.03	0.91 (0.00)	H_1: $\beta < 1$	71	0.00
L25 Gnathion to hind border of preorbital process	73	0.89 ± 0.11	0.68 ± 0.02	0.92 (0.00)	NA	NA	NA
L26 Height of skull at bottom of mastoid	61	1.40 ± 0.20	0.63 ± 0.04	0.90 (0.00)	NA	NA	NA
L27 Height of sagittal crest	55	–	–	0.73 (0.00)	–	–	–

Mandibular

M28 Length of mandible	74	1.58 ± 0.09	0.69 ± 0.02	0.94 (0.00)	H_1: $\beta < 1$	72	0.00
M29 Length of mandibular tooth row	64	1.70 ± 0.12	0.49 ± 0.02	0.85 (0.00)	H_1: $\beta < 1$	62	0.00
M30 Length of lower postcanine row	69	1.96 ± 0.11	0.36 ± 0.02	0.83 (0.00)	H_1: $\beta < 1$	67	0.00
M31 Height of mandible at meatus	72	-1.45 ± 0.19	1.06 ± 0.04	0.93 (0.00)	H_1: $\beta > 1$ ns	70	0.26
M32 Angularis to coronoideus	70	-0.89 ± 0.17	0.95 ± 0.03	0.94 (0.00)	H_1: $\beta > 1$ ns	68	0.28

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APPENDIX 3. 'Robust' least squares straight line equations, Spearman rank-order correlation coefficients, and allometry for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on log condylobasal length. Hypothesis testing on regression slopes as for Appendix 2.

Dependent variable	n	Linear regression			Allometry		
		Intercept ± S.E.	Slope ± S.E.	r (p)	Alternative hypothesis	d.f.	p
Dorsal							
D2 Gnathion to middle of occipital crest	79	-0.22 ± 0.17	1.01 ± 0.03	0.97 (0.00)	NA	NA	NA
D3 Gnathion to posterior end of nasals	80	-2.01 ± 0.19	1.18 ± 0.04	0.95 (0.00)	H_1: ß > 1	78	0.00
D4 Greatest width of anterior nares	79	-2.62 ± 0.32	1.08 ± 0.06	0.87 (0.00)	H_1: ß > 1 ns	77	0.18
D5 Greatest length of nasals	78	-3.21 ± 0.31	1.27 ± 0.06	0.88 (0.00)	H_1: ß > 1	76	0.00
D6 Breadth at preorbital processes	78	-2.19 ± 0.21	1.16 ± 0.04	0.92 (0.00)	H_1: ß > 1	76	0.00
D7 Least interorbital constriction	78	-3.36 ± 0.30	1.27 ± 0.06	0.89 (0.00)	H_1: ß > 1	76	0.00
D8 Breadth at supraorbital processes	74	-1.66 ± 0.34	1.03 ± 0.06	0.83 (0.00)	NA	NA	NA
D9 Breadth of brain case	80	3.48 ± 0.19	0.17 ± 0.03	0.39 (0.00)	NA	NA	NA
Palatal							
P10 Palatal notch to incisors	82	-1.22 ± 0.20	1.07 ± 0.04	0.89 (0.00)	NA	NA	NA
P11 Length of upper postcanine row	82	-0.54 ± 0.23	0.84 ± 0.04	0.77 (0.00)	NA	NA	NA
P12 Greatest bicanine breadth	82	-2.38 ± 0.26	1.14 ± 0.05	0.93 (0.00)	H_1: ß > 1	80	0.00
P13 Gnathion to posterior end of maxilla	82	-1.06 ± 0.11	1.06 ± 0.02	0.96 (0.00)	H_1: ß < 1 ns	NA	NA
P14 Breadth of zygomatic root of maxilla	83	-1.97 ± 0.48	0.85 ± 0.09	0.75 (0.00)	H_1: ß = 1 ns	81	0.17
P15 Breadth of palate at postcanine 1	73	-4.89 ± 0.48	1.47 ± 0.09	0.89 (0.00)	H_1: ß > 1	71	0.00
P16 Breadth of palate at postcanine 3	73	-2.42 ± 0.35	1.04 ± 0.06	0.87 (0.00)	H_1: ß > 1 ns	71	0.56
P17 Breadth of palate at postcanine 5	80	-3.11 ± 0.34	1.20 ± 0.06	0.85 (0.00)	H_1: ß > 1	78	0.001
P18 Gnathion to hind border of postglenoid process	77	-1.18 ± 0.12	1.16 ± 0.02	0.96 (0.00)	NA	NA	NA
P19 Bizygomatic breadth	83	-1.25 ± 0.21	1.12 ± 0.04	0.89 (0.00)	NA	NA	NA
P20 Basion to zygomatic root (anterior)	81	-0.16 ± 0.08	0.96 ± 0.02	0.97 (0.00)	NA	NA	NA
P21 Calvarial breadth	81	-0.76 ± 0.16	1.00 ± 0.03	0.94 (0.00)	NA	NA	NA
P22 Mastoid breadth	81	-2.22 ± 0.17	1.29 ± 0.03	0.95 (0.00)	NA	NA	NA
P23 Basion to bend of pterygoid	81	0.89 ± 0.12	0.63 ± 0.02	0.90 (0.00)	H_1: ß < 1	79	0.00

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Lateral

L24 Gnathion to foramen infraorbital	82	-2.61 ± 0.17	1.26 ± 0.03	0.94 (0.00)	NA	NA	NA
L25 Gnathion to hind border of preorbital process	82	-2.49 ± 0.14	1.25 ± 0.03	0.97 (0.00)	NA	NA	NA
L26 Height of skull at bottom of mastoid	70	-1.90 ± 0.32	1.19 ± 0.06	0.94 (0.00)	NA	NA	NA
L27 Height of sagittal crest	60	–	–	0.80 (0.00)	–	–	–

Mandibular

M28 Length of mandible	82	-1.58 ± 0.10	1.22 ± 0.02	0.98 (0.00)	NA	NA	NA
M29 Length of mandibular tooth row	73	-0.61 ± 0.19	0.88 ± 0.04	0.85 (0.00)	$H_1: \beta < 1$	71	0.002
M30 Length of lower postcanine row	78	0.22 ± 0.18	0.66 ± 0.03	0.84 (0.00)	$H_1: \beta < 1$	76	0.00
M31 Height of mandible at meatus	81	-6.31 ± 0.32	1.88 ± 0.06	0.95 (0.00)	$H_1: \beta > 1$	79	0.00
M32 Angularis to coronoideus	79	-5.11 ± 0.28	1.66 ± 0.05	0.95 (0.00)	$H_1: \beta > 1$	77	0.00

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APPENDIX 4. 'Robust' least squares straight line equations and Spearman rank-order correlation coefficients for log dorsal (D1–9), palatal (P10–23), lateral (L24–27) and mandibular (M28–32) skull measurements on age (y)

Dependent variable	n	Linear regression		
		Intercept ± S.E.	Slope ± S.E.	r (p)
Dorsal				
D1 Condylobasal length	51	5.15 ± 0.02	0.04 ± 0.00	0.89 (0.00)
D2 Gnathion to middle of occipital crest	49	4.97 ± 0.02	0.04 ± 0.00	0.92 (0.00)
D3 Gnathion to posterior end of nasals	49	4.04 ± 0.02	0.05 ± 0.00	0.87 (0.00)
D4 Greatest width of anterior nares	49	2.95 ± 0.03	0.04 ± 0.00	0.81 (0.00)
D5 Greatest length of nasals	47	3.30 ± 0.03	0.05 ± 0.00	0.76 (0.00)
D6 Breadth at preorbital processes	50	3.77 ± 0.02	0.05 ± 0.00	0.87 (0.00)
D7 Least interorbital constriction	49	3.09 ± 0.03	0.06 ± 0.00	0.89 (0.00)
D8 Breadth at supraorbital processes	45	3.60 ± 0.03	0.05 ± 0.00	0.85 (0.00)
D9 Breadth of brain case	51	4.38 ± 0.01	0.01 ± 0.00	0.31 (0.00)
Palatal				
P10 Palatal notch to incisors	50	4.24 ± 0.03	0.05 ± 0.00	0.84 (0.00)
P11 Length of upper postcanine row	50	3.78 ± 0.03	0.03 ± 0.00	0.59 (0.00)
P12 Greatest bicanine breadth	50	3.48 ± 0.02	0.05 ± 0.00	0.87 (0.00)
P13 Gnathion to posterior end of maxilla	50	4.36 ± 0.02	0.04 ± 0.00	0.83 (0.00)
P14 Breadth of zygomatic root of maxilla	52	2.45 ± 0.03	0.03 ± 0.00	0.57 (0.00)
P15 Breadth of palate at postcanine 1	43	2.57 ± 0.03	0.07 ± 0.00	0.89 (0.00)
P16 Breadth of palate at postcanine 3	43	2.89 ± 0.03	0.04 ± 0.00	0.77 (0.00)
P17 Breadth of palate at postcanine 5	49	3.05 ± 0.03	0.05 ± 0.00	0.74 (0.00)
P18 Gnathion to hind border of postglenoid process	46	4.79 ± 0.02	0.05 ± 0.00	0.92 (0.00)
P19 Bizygomatic breadth	51	4.50 ± 0.02	0.05 ± 0.00	0.89 (0.00)
P20 Basion to zygomatic root (anterior)	49	4.77 ± 0.02	0.04 ± 0.00	0.90 (0.00)
P21 Calvarial breadth	51	4.36 ± 0.02	0.04 ± 0.00	0.89 (0.00)
P22 Mastoid breadth	50	4.37 ± 0.02	0.06 ± 0.00	0.91 (0.00)
P23 Basion to bend of pterygoid	50	4.14 ± 0.02	0.02 ± 0.00	0.75 (0.00)

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Lateral				
L24 Gnathion to foramen infraorbital	51	3.88 ± 0.03	0.05 ± 0.005	0.81 (0.00)
L25 Gnathion to hind border of preorbital process	50	3.92 ± 0.03	0.05 ± 0.00	0.87 (0.00)
L26 Height of skull at bottom of mastoid	39	4.17 ± 0.03	0.05 ± 0.005	0.79 (0.00)
L27 Height of sagittal crest	38	–	–	0.86 (0.00)
Mandibular				
M28 Length of mandible	50	4.70 ± 0.02	0.05 ± 0.00	0.91 (0.00)
M29 Length of mandibular tooth row	48	3.89 ± 0.02	0.04 ± 0.00	0.75 (0.00)
M30 Length of lower postcanine row	47	3.59 ± 0.02	0.03 ± 0.00	0.76 (0.00)
M31 Height of mandible at meatus	49	3.31 ± 0.04	0.08 ± 0.01	0.90 (0.00)
M32 Angularis to coronoideus	48	3.42 ± 0.03	0.07 ± 0.00	0.88 (0.00)
Log body length	44	4.53 ± 0.03	0.07 ± 0.00	0.87 (0.00)

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APPENDIX 5. Spearman rank-order correlation coefficients for log skull variables according to region. Symbol * denotes that the correlation is significant at the 0.05 level with the total sample size in brackets ().

Frontal

	Var (D7)	Var (D8)
Var (D7)	1.00 (79)	0.93 (71)
Var (D8)	0.93 (71)	1.00 (75)

Nasal

	Var (D4)	Var (D5)
Var (D4)	1.00 (79)	0.81* (76)
Var (D5)	0.81* (79)	1.00 (78)

Neurocranium

	Var (D9)	Var (L27)
Var (D9)	1.00 (80)	0.25 (59)
Var (L27)	0.25 (59)	1.00 (60)

Zygomatic arch

	Var (P14)	Var (P19)
Var (P14)	1.00 (83)	0.71* (83)
Var (P19)	0.71* (83)	1.00 (83)

Basicranium

	Var (P21)	Var (P22)	Var (P23)
Var (P21)	1.00 (82)	0.97 (80)	0.88 (80)
Var (P22)	0.97 (80)	1.00 (82)	0.85 (81)
Var (P23)	0.88 (80)	0.85 (81)	1.00 (82)

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Splanchnocranium

	Var (D3)	Var (L24)	Var (L25)
Var (D3)	1.00 (80)		
Var (L24)	0.94* (79)	1.00 (82)	
Var (L25)	0.96* (80)	0.98* (81)	1.00 (82)

Mandible

	Var (M28)	Var (M29)	Var (M30)	Var (M31)	Var (M32)
Var (M28)	1.00 (83)				
Var (M29)	0.83 (73)	1.00 (74)			
Var (M30)	0.79 (78)	0.92 (69)	1.00 (79)		
Var (M31)	0.88 (81)	0.82 (72)	0.78 (78)	1.00 (82)	
Var (M32)	0.88 (79)	0.80 (71)	0.80 (76)	0.97 (80)	1.00 (80)

Palate

	Var (P10)	Var (P11)	Var (P12)	Var (P13)	Var (P15)	Var (P16)	Var (P17)
Var (P10)	1.00 (82)						
Var (P11)	0.76* (81)	1.00 (82)					
Var (P12)	0.84* (81)	0.76* (81)	1.00 (82)				
Var (P13)	0.91* (81)	0.79* (81)	0.90* (81)	1.00 (82)			
Var (P15)	0.79* (81)	0.76* (72)	0.93* (73)	0.84* (72)	1.00 (73)		
Var (P16)	0.78* (72)	0.76* (72)	0.95* (73)	0.84* (72)	0.93* (72)	1.00 (73)	
Var (P17)	0.75* (79)	0.64* (79)	0.91* (80)	0.83* (79)	0.93* (72)	0.95* (71)	1.00 (80)

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